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N. Rashevsky

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STUDIES IN THE PHYSICOMATHEMATICAL THEORY OF ORGANIC FORM

N. RASHEVSKY
THE UNIVERSITY OF CHICAGO

In continuation of previous studies the theory is developed on the assumption that the form of any organism is determined by requirements to perform definite biological functions. A previously outlined theory of the form of plants is developed further, showing how the conditions of mechanical strength together with the specifications of the total mass and metabolism, may quantitatively determine not only the general form of the plant, but even the number, size, shape and shades of the leaves. Next the form of animals, as required by mechanical conditions and by the different types of possible locomotions is discussed. A mathematical theory of locomotion of snakes in relation to their shape is outlined. Next is discussed the form and locomotion of quadrupeds. A number of theoretical relations, which describe the shape of an animal, are derived and compared to available observations. After that the theory of flight of birds and insects is discussed, and again some form relations comparable with observations, are discussed. Finally a set of equations is outlined, which determines not only the external shape, but also the internal structure of animals. Different relations pertaining to some inner organs are derived and compared with available observations. The paper ends with a brief discussion on the shape of unicellular organisms.

Introduction

The problem of organic form is justly considered as one of the most difficult problems of biology. Rather pessimistic views as to the possibility of a physicomathematical treatment of that problem have been expressed not only by some philosophically minded biologists (L. v. Bertalanffy, 1928), but even by such physicochemically oriented investigators as A. Meyerhoff (1926). A definite doubt as to whether the problem of form lies at all within the scope of physics is felt through many of the arguments. The physicist of course knows that such skepticism is not justified. Not only does crystallography offer a problem of form in physics, but whenever a physicist deals with *fields*, such as diffusion fields, electromagnetic fields or others, questions of spatial relations, and hence of form, enter explicitly.

In view of the importance of the diffusion fields in biology, N. Rashevsky (1929) has indicated a mathematical approach to the problem of organic form by considering the combined effects of diffusion field and surface tensions. Later on the theory was amplified by the

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introduction of diffusion drag forces (Rashevsky, 1938, 1940) which threw some light on the form of single cells.

A rough attempt to develop a physico-mathematical theory of the form of metazoan animals was made by Rashevsky (1933), who arrived at a gross theoretical classification of some existing forms. Subsequently he proposed an improved theory (Rashevsky, 1938, Chapter xiv), which so far remained only an outline. The principal reason for that was a realization that although a reduction of the problem of organic form to physico-chemical interactions may be possible *in principle,* the working out of actual specific instances would be so complex, as to make the task technically hopeless. Therefore recently Rashevsky (1943a) proposed a different approach to the whole problem, seeking to solve it by the introduction of one or a few simple *formal* principles or postulates, which need not *immediately* be reduced to a physicochemical mechanism. Such a procedure is not unfamiliar to a physicist.

The postulate proposed by Rashevsky is that the geometric form of any organism is determined by the requirements of certain biological functions. Since these are almost innumerable, it is proposed, for the beginning, to limit the theory to a few of the simplest ones. As such, the metabolic level, the speed of locomotion and the amount of nervous coordination have been suggested. Given an organism of a mass M, average metabolism q ergs per unit mass, average amount of nervous tissue nM, the average velocity of locomotion v will be determined by the geometrical structure of the organism. In general however, the same results may be obtained by different structures. Therefore, to make the problem definite, Rashevsky introduces a new principle, namely, that of all the structures which give us the desired functions, the simplest one actually occurs in nature. This of course requires a proper definition of simplicity.

In the case of plants, in which usually we may put $v = 0$ and $n = 0$, the form is to be determined by the considerations of mechanical strength and of sufficient size of food conductors, which enable the plant to have a given metabolic rate q for a given mass M.

In the above mentioned papers, Rashevsky has outlined very roughly how the theory is to be developed. In case of animals, terrestrial locomotion without extremities is limited as to speed. Only animals with low velocity of locomotion, will be possible without extremities (snakes, worms). In that case the ratio of length to width of the animal and hence its shape is determined by M, q and v. Higher velocities of locomotion may be obtained with either four or two extremities. Though the second case is structurally simpler, it requires much more nervous coordination, since standing on two legs is mechanically an unstable process. Hence, where the necessary coordination is not sufficient for maintaining a posture on two extremities, quadruped forms result. The size of extremities is determined by M , q and v .

In this paper we propose to elaborate further the above suggestions and derive more relations, which determine the shapes of plants and animals. It must however be emphasized, that in this study we still remain largely on a purely abstract, theoretical level. The actual situations are much more complex. As in other branches of mathematical biophysics, we must start with idealized, oversimplified cases and study at first *all conceivable* situations though some of them may never occur in nature. Only when a great many of such conceivable situations have been studied will a comparison of the theory with observations indicate which of the situations actually occur.

Although in deriving any relations from too abstract and oversimplified assumptions we should not expect those relations to hold actually, nevertheless, even in such cases a mathematically derived relation may at least very roughly approximate reality. Therefore, wherever possible, we shall make comparisons between theory and observations. We must however constantly keep in mind, that whenever such comparisons show any agreement between theory and observations, this is not to be considered as constituting any proof of the theory, but rather as an illustration of what the theory *may* do and as a stimulus for further theoretical and experimental research.

It is of course impossible to cover at this stage the whole field of organic form. We shall therefore confine ourselves to a few selected topics. In section *I* we shall give a rather abstract theory of the form of plants, extending the previous studies (Rashevsky, 1943d). Section *II* deals with some types of locomotion of snakes in relation to their form. In section *III* we pass to the consideration of quadrupeds. From considerations of mechanical strength we shall derive two relations which partly determine the form of the animal. In section *IV, V* and *VI,* the terrestrial locomotion of quadrupeds and bipeds is discussed in relation to their form, and another relation, determining the shape of the animal is derived. Section *VII* deals with the flight of birds and insects as related to their general shape. Finally in section *VIII* the relations of some physiological functions of the organism to its internal structure are discussed and several quantitative expressions derived, which determine that internal structure. Thus not only the external form but also the internal structure of animals is taken within the scope of this study. We conclude with a brief discussion of forms of unicellular organisms.

I. Forms of Plants

It has been shown by N. Rashevsky (1943a) that to some extent the general shape of a plant may be determined by the mass M and metabolism qM, principally from mechanical considerations. Denoting by l_0 the length of the main trunk, by r_0 its radius, by l and r the average length and radii of the branches, by n the total number of branches and by δ the average density of the plant, Rashevsky established six general equations for the determination of those six quantities in terms of q and M. By making specific assumptions about some functions, which were left originally indeterminate, Rashevsky (1943d) arrives at explicit expressions for the above six quantities. But five of those largely determine the gross shape of the plant. Small l_0 and r_0 and large n, give us a bush. Small l_0, large r_0, small n and large l correspond to a form of an apple tree, while large l_0, r_0, and n but small l and r produce a tree like a poplar (Rashevsky, 1943d). Two pathways are open for further studies. One is to refine the specific assumptions made by Rashevsky (1943d) and compare the theoretical results with possible measurements on plants. The other is to remain on the abstract level, and to investigate to what extent further details of the structure of a plant may be determined by M and q alone. We shall here follow the second pathway.

It is very doubtful whether actually M and q are the only independent variables, which determine the shape of a plant. Actually, the metabolic processes differ in different plants, and q represents therefore a sort of an average quantity. More detailed specifications of the qualitative character of the total metabolism will actually have to be given. Environmental factors also probably play a role. Since we remain at present on a purely abstract theoretical level, it is of interest to show to what extent M and q alone *may* determine the details of a plant's external structure.

Besides the variables introduced above, let us introduce the following additional ones: Δ_1—the *average* length of a leaf, Δ_2—its average width, m—the total number of leaves, d—the length of the leaf-stalk, r_2—its radius, r_3—the average radius of the vein of a leaf, and n'—the average number of veins per leaf. For simplicity let us consider the thickness of a leaf as a constant, so that its mass is approximately proportional to $\Delta_1\Delta_2$. We also shall at first consider only branches of first order. Higher order branches will be introduced subsequently.

As before, (Rashevsky, 1943d) we have the following equation for the total mass:

$$M = \pi\delta\,(l_0 r_0^2 + nlr^2). \tag{1}$$

The total metabolism being assumed to be proportional to the total area of the leaves, we now have, denoting by k a constant

$$qM = k\Delta_1\Delta_2 m\,. \tag{2}$$

The length of a branch is limited by its mechanical strength and its mass. The latter is a function of the size of the branch and of the mass of all the leaves on the branch. We therefore have a relation of the form:

$$l = f\left(r\,,\,\delta\,,\,\frac{m}{n}\,\Delta_1\Delta_2\right). \tag{3}$$

Mechanical considerations give us again the relation

$$l_0 = f_0(r_0\,,\,\delta\,,\,M). \tag{4}$$

The requirement that the cross-section of the trunk and of each branch should be sufficient to allow ample flow of metabolites gives (Rashevsky, 1943a, d):

$$r_0 = f_1(qM\,,\,\delta), \tag{5}$$

$$r = f_1\left(\frac{qM}{n},\ \delta\right). \tag{6}$$

The number of leaves along the axis of a branch is limited by the width Δ_2 of the leaf and is of the order of l/Δ_2. The number of leaves that may be arranged along the circumference of a branch is also limited by Δ_2. It is of the order of $2\pi(r + d + \dfrac{\Delta_1}{2})/\Delta_2$, since $2\pi(r + d + \Delta_1/2)$ is the length of the circumference along which the centers of the leaves are arranged. Hence denoting by a_1 a coefficient of proportionality, the total number m/n of leaves per branch is of the form

$$m/n = 2\pi a_1(r + d + \Delta_1/2)\,l/\Delta_2^{\,2}. \tag{7}$$

The distance between the branches along the trunk is of the order of magnitude of $d + \Delta_1$, or is proportional to it. The total number of branches that can be arranged on the same level of the trunk is approximately $\pi r_0/r$. Hence the total number of branches is approximately

$$n = \pi r_0 l_0/r(d + \Delta_1). \tag{8}$$

A consideration similar to the one which leads to equations (5) and (6) gives:

$$r_2 = f_2(qM/m)\,; \tag{9}$$

while consideration of mechanical strength leads to a relation:

$$d = f_3(r_2, \Delta_1\Delta_2). \tag{10}$$

The cross section of each vein must be such as to permit the flow of necessary metabolites. The metabolism per vein being qM/mn' we have a relation

$$r_3 = f_4(qM/mn'). \tag{11}$$

Since the metabolites flow into the leaf through the surface of the vein, which is approximately $2\pi r_3\Delta_2$, since $\Delta_2/2$ is approximately the length of a vein, that surface must be of such a size as to permit the proper flow. The principle of maximum simplicity suggests that that surface be a constant multiple of the size necessary to permit the proper flow. We therefore have a relation:

$$\frac{qM}{mn'} = f_5(\Delta_2 r_3). \tag{12}$$

Finally the mass of all the veins may be assumed not to exceed a certain fraction of the total mass of the leaf. Or we may introduce again considerations of mechanical strength, since the veins form part of the supporting framework of a leaf. In either case we get a relation of the form

$$f_6(\Delta_1, \Delta_2, r_3, n') = 0. \tag{13}$$

Altogether we have (13) equations for the determination of the 13 varieties $l_0, r_0, n, l, r, \delta, \Delta_1, \Delta_2, m, d, r_2, r_3, n'$.

If we assume that the metabolism of a leaf is proportional to its chlorophyll content, then we must consider the constant k in equation (2) as proportional to that content. We may leave k as a third independent variable, which by the way, determines the lighter or darker shade of a leaf. With proper choice of the different functions involved in the above equations, it may happen that those equations will have solutions only for values of k, lying within a relatively narrow range $k_1 < k < k_2$. This may account for the circumstance that we do not have a too wide variation of shades in leaves. Saprophyte plants will have to be treated separately, and do not fall within the scope of this theory.

It has been suggested (Rashevsky, 1943a) that the metabolic rate of a leaf may determine its finer shape. If for a large k, and large Δ_1 and Δ_2, n' turns out to be small, the leaf may not receive enough metabolites at the remotest points. Therefore, while for large values of n' a form of Figure 1a will occur, for small n' only the form of Figure 1b will be possible. Hence large k, Δ_1 and Δ_2, but small n' give us dented leaves, while small k, Δ_1 and Δ_2, and large n' give us smooth-edged leaves. But with a large k and very large n' the leaf will have a smooth edge, while small k and very small n' will give a dented edge.

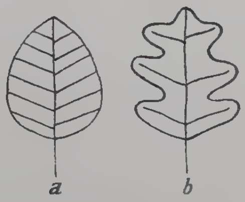

FIGURE 1

As emphasized above, the assumptions underlying this outline do not need to be true. The important result is that a variety of plant forms *may* conceivably be determined in great detail by considerations of relatively simple biological functions. The next step to take is to make specific assumptions about different functions which have been left indefinite, and to see to what extent explicit expressions thus obtained will agree with observations. After that we should investigate theoretically the effect of the individual metabolic reactions, thus introducing instead of one q, several independent variables. Instead of a single average δ, several such quantities may have to be introduced for the different parts of a plant. Thus step by step we may approach a theory that will cover a number of actual observations.

We shall conclude this section by indicating how branches of higher order may be taken into account. For simplicity let us limit ourselves to considerations of branches only, as has been done before (Rashevsky, 1943a, d), omitting the problem of leaves. The above considerations which comprise the role of the leaves may then be readily combined with the following ones.

Consider n_1 first order branches and n_2 second order branches. Let l_1, l_2, r_1, r_2 be their corresponding lengths and radii.

We now have:

$$M = \pi\delta\,(l_0 r_0^2 + n_1 l_1 r_1^2 + n_2 l_2 r_2^2), \tag{14}$$

and

$$qM = k\,(n_1 l_1 r_1 + n_2 l_2 r_2). \tag{15}$$

Each first order branch carries n_2/n_1 second order branches. Hence the weight of each first order branch plus all second order branches which it carries, is

$$\pi\delta\,(l_1r_1^2 + \frac{n_2}{n_1}\,l_2r_2^2)\,.$$

For mechanical strength we must have:

$$r_1 = f[\delta\,,\,(l_1r_1^2 + \frac{n_2}{n_1}\,l_2r_2^2)]\,, \tag{16}$$

and similarly

$$r_2 = f\,(\delta, l_2r_2^2)\,. \tag{17}$$

We also have equations corresponding to equations (4) and (5). Moreover we have

$$r_1 = f_1(\frac{qM}{n_1}, \delta) \tag{18}$$

and

$$r_2 = f_1(\frac{qM}{n_2}, \delta)\,. \tag{19}$$

Altogether we have eight equations for the nine variables: δ, l_0, r_0, n_1, r_1, l_1, n_2, r_2, l_2. The ninth equation is provided by the requirement that the length l_2 of the second order branches should be of the order of the distance between the first order branches (Figure 2). The number of branches of first order that can be placed at the

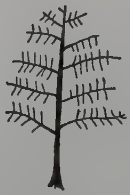

FIGURE 2

same level around the circumference of the trunk is

$$2\pi r_0/2r_1 = \pi r_0/r_1\,.$$

If x is the distance along the trunk between first order branches, then we have:

$$n_1 = \frac{\pi r_0}{r_1}\,\frac{l_0}{x}\,,$$

putting $l_2 = a_2 x$, a_2 being a coefficient of proportionality, we find:

$$l_2 = \frac{a_2 \pi r_0 l_0}{r_1 n_1}, \qquad (20)$$

which gives us the ninth equation.

If we consider third order branches, we introduce three new variables n_3, r_3, l_3, the number, length and radius of the third order branches. This introduces additional terms into equations (14), (15) and (16). Moreover, we obtain two new relations for r_3, which correspond to equations (17) and (19). And a third new relation is obtained by postulating that the l_3 should be a given fraction of the distance between second order branches. Thus we shall have sufficient additional relations for the determination of the additional variables. The process may be extended to branches of any order.

II. Locomotion and Form of Snakes

There are apparently at least three different types of locomotions of snakes (Mosauer, 1931, 1932). Of those we shall consider the one which is regarded as the most common one. According to Mosauer the snake assumes an approximately sinusoidal shape and moves forward in such a way, that each point along the body follows the same sinusoidal path. The physical mechanism of such a locomotion seems at first somewhat puzzling. As we shall presently see, however, this type of locomotion may be obtained by assuming that the coefficients of static friction of the snake against the ground are different in the direction of the body axis and in the direction normal to it. The reasons for such a possibility will be discussed presently.

Inasmuch as the exact shape of the curve formed by the body of the snake has never been ascertained, and may in a strict mathematical sense be not a sinusoid at all, we shall in the following discussion make some very crude approximations, by assuming instead of a smooth wavy line a zigzag line (Figure 3), of total length L. The expressions derived are more of the nature of dimensional relations

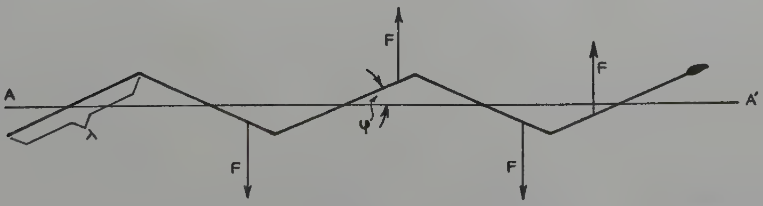

FIGURE 3

and establish orders of magnitudes, rather than exact equations. However, even those rough approximations throw interesting light on the problem. Let the length of each straight segment be λ. Let at every point a muscular force f per unit length tend to displace the different parts of the body at a right angle to AA', as shown by the arrows (Figure 3). The component of this force along the snake's axis is

$$f_l = f \sin\phi; \tag{1}$$

the component normal to the direction of the body axis is

$$f_n = f \cos\phi. \tag{2}$$

Let the static friction r_l for displacement along the axis be less than the static friction r_n for displacement perpendicular to that axis:

$$r_l < r_n. \tag{3}$$

This may be due to either a peculiarity of the surface of the skin of the snake, or to the fact that the snake, due to its weight, makes an impression in the ground. Such an impression tends to prevent lateral displacements. Longitudinal displacements may be easier, because of the wedge-like action of the snake's head. The total force acting along the snake's axis is

$$F_l = f_l L = fL \sin\phi. \tag{4}$$

The total force acting normally to the axis is

$$F_n = f_n L = fL \cos\phi. \tag{5}$$

If

$$F_n < r_n; \ F_l > r_l, \tag{6}$$

then the body of the snake will glide along its own axis. Let the velocity of this gliding be v cm sec^{-1}.

A zigzag, or a wave-line shape of the body of the snake is produced by contraction of muscles on the "concave" sides of each "peak", and by relaxation of the muscles on the "convex" side of it. Hence if the body of the snake glides along its axis with the velocity v, a wave of contraction must move along the body of the snake with the same velocity v. If the zigzag line is periodical, as we shall consider to be the case, then, denoting by 2λ the wave length, this contraction wave will have a period

$$T = 2\lambda/v. \tag{7}$$

or a frequency

$$\nu = v/2\lambda. \tag{8}$$

The dry friction of the moving snake against the ground being independent of the velocity, any force acting along the axis, which is strong enough to set the body in motion, will keep this motion accelerated indefinitely, if other limiting factors do not enter into play. In the present case such a limiting factor is found in the condition, that as the snake moves along its axis with the velocity v, a contraction wave must move along its muscles with the same velocity. A snake can not move with respect to the ground with a velocity larger than the velocity of the contraction wave with respect to its body. Thus the factors limiting the velocity of the snake must be sought in the properties of the snake's muscular apparatus.

From (8) we have:

$$v = 2\lambda\nu . \tag{9}$$

Since $2\lambda < L$, the velocity v of the contraction wave is limited fundamentally by ν. This latter is probably limited by the viscosity of the muscle (A. V. Hill, 1927). The greater ν, the faster must be the velocity u of contraction of the muscle, and that velocity is limited by the viscosity.

As an illustration we may consider the following line of thought. For a viscous rod of length l, cross section s^2, viscosity η, we have

$$\frac{1}{l}\frac{dl}{dt} = \frac{1}{3\eta}\frac{F}{s^2} \tag{10}$$

where F is the total force. Hence, if a denotes a constant and

$$F = as^2, \tag{11}$$

as happens to be approximately the case with muscles, then

$$u = \frac{dl}{dt} = \frac{al}{3\eta}. \tag{12}$$

The greater the amplitude A of the wave, the larger must be the relative shortening Δl of the muscles. It is also larger, the greater the thickness s of the body of the snake. Moreover, the smaller the wavelength the larger the curvature of the body and therefore the larger Δl. Hence

$$\Delta l \propto As/\lambda , \tag{13}$$

and

$$u \infty \frac{\Delta l}{T} = \nu\Delta l \propto \frac{As}{\lambda}\nu. \tag{14}$$

Since the length l of the contracting mass of muscles is of the order of λ,

$$l \infty \lambda, \tag{15}$$

hence, from (12):

$$u \propto a\lambda/3\eta. \tag{16}$$

Equations (14) and (16) give

$$As\nu \propto a\lambda^2/3\eta, \tag{17}$$

or

$$\nu \propto a\lambda^2/3A\eta s. \tag{18}$$

Introducing this into (9), and making the plausible assumption that

$$\lambda \propto L, \tag{19}$$

we have

$$v \propto 2aL^3/3A\eta s. \tag{20}$$

The force f per unit length may be assumed to be proportional to s^2, because of its approximate proportionality to the cross section of the muscles. If we increase s, we increase both the circumference and the thickness of the muscles. Hence, their cross section varies approximately as s^2. Hence, denoting by a_1 a constant

$$f = a_1 s^2 \tag{21}$$

Therefore (4) and (6) give

$$a_1 s^2 L \sin\phi \geqq r_l, \tag{22}$$

or

$$\sin\phi \geqq \frac{r_l}{a_1 s^2 L} = \frac{r_l}{a_1 V} \tag{23}$$

where V is the volume of the snake.

But, from Figure 3,

$$A \infty \lambda \sin\phi, \tag{24}$$

hence

$$A \infty \lambda r_l / a_1 V. \tag{25}$$

Introducing (25) into (20) we find, remembering (15) and (19):

$$v \infty L^2 V/\eta s r_l. \tag{26}$$

The quantity v is the velocity of the snake along its axis. Along AA' the velocity is

$$\bar{v} = v \cos\phi. \tag{27}$$

Since the density of the snake is close enough to one, we have from (23):

$$\sin\phi = \frac{r_l}{a_1 M}, \tag{28}$$

hence

$$\cos\phi = \sqrt{1 - \frac{r_l^2}{a_1^2 M^2}}. \tag{29}$$

Therefore (26) and (27) give

$$\bar{v} \propto \frac{L^2 M}{\eta s r_l}\sqrt{1 - \frac{r_l^2}{a_1^2 M^2}}. \tag{30}$$

Since

$$L s^2 = M, \tag{31}$$

s may be eliminated from (30), and this determines L in terms of M and V; s is then determined from (31). *Hence* v *and* M, *determine the shape of the snake.*

It seems paradoxical that $\bar{v}$ should increase with M. If r_l increases itself with M, the latter may drop out of the equation.

The weakest points in the reasoning are relations (13) and (15). In (13) we may perhaps consider instead of λ the length of the individual muscles. This will introduce a parameter characterizing the inner anatomical structure. Instead of (15) a more exact relation should be established.

A more rigorous procedure would be to establish from more exact considerations of the viscous losses a maximum value of ν in terms of λ, a relation to replace (18). Let the relation be

$$\nu = \nu(\lambda)$$

then the exact equation (9) gives

$$\nu = 2\lambda\nu(\lambda). \tag{32}$$

It may happen, that $\lambda\nu(\lambda)$ has a maximum for $\lambda_m << L$. In this case the equation

$$d[\lambda\nu(\lambda)]/d\lambda = 0 \tag{33}$$

may be considered as determining the actual value of λ.

The physical reason why $\bar{v}$ increases with M is due to the fact that with the assumption made, the total force is proportional to M [equations (4) and (21)], while the viscous resistance increases with L, and decreases with s.

It must also be kept in mind, that the above considerations hold only for uniform motion. The acceleration at the beginning will be expressed in a more complicated way, and it seems likely that, at least approximately, the acceleration will not depend on M.

If we wish to connect the velocity of locomotion to the available metabolic energy Mq, we must compute for a given ν and λ, and hence v, the energy losses E per unit time, and also remember that the energy loss due to friction against ground is $r_l v$ erg sec^{-1}. Hence

$$E + r_l v = Mq. \tag{34}$$

If E is known as a function of v, equation (34) determines the latter in terms of M and q.

Since the actual values of r_l and r_n, as well as of other constants are not known, it is impossible at present to compute the limiting speed of locomotion for a given q. It appears plausible, however, that due to the very large frictional area, those speeds would be low. According to Mosauer (1931) the largest observed speeds of snakes are of the order of 1 meter per second. To obtain higher speeds, different bodily structures must be used, involving extremities.

A further improvement of the above outlined theory would consist in considering instead of a zigzag line a continuous line. One might then investigate what kind of continuous periodical line gives a maximum velocity, other parameters being kept constant. In any case the possible relation between the size and shape of snakes and their speed should be made the object of careful quantitative studies.

III. Some General Considerations on the Shape of Quadrupeds

In a very rough way, a quadruped may be considered from a mechanical point of view as a bar supported at its ends. This sets definite limits to the length of the trunk for a given width. The actual supporting structure is the vertebral column. However, not only the ribs, but even the soft muscular and other tissues contribute to some extent to the mechanical strength of the trunk. The study of different factors and conditions affecting the mechanical strength of the trunk of quadrupeds is a most interesting, but extremely complex problem. Its development will result in many relations which will offer clues for biometric studies.

We shall not tackle that general problem at present. Inasmuch as we are as yet confining our study to extremely oversimplified pictures, we shall, *for the sake of illustration only,* investigate the situation that would prevail if the trunk of a quadruped could be considered as a uniform bar of length L and width W, supported at its ends.

If such a bar is uniformly loaded with a load p per unit length, then the sagging f in the middle is (Geckeler, 1928, p. 166) equ. 16):

$$f \propto pL^4/W^4\,, \tag{1}$$

hence the relative sagging

$$f/L \propto pL^3/W^4\,. \tag{2}$$

By definition

$$p = M/L\,, \tag{3}$$

where M is the mass of the trunk, which approximately may be set equal to the total mass of the animal. Hence

$$f/L \propto ML^2/W^4\,. \tag{4}$$

The relative sagging should not exceed a certain threshold value, lest the bar breaks. Assuming this value to be a constant, and that f/L is always a given fraction of that constant, we have:

$$ML^2/W^4 = \text{Const. or } L^2/W^4 \propto M^{-1}\,. \tag{5}$$

Moreover, we have approximately

$$LW^2 = M\,. \tag{6}$$

Expressions (5) and (6) give

$$L \propto M^{1/4};\, W \propto M^{3/8};\, \frac{L}{W} \propto M^{-1/8};\, W \propto L^{3/2}. \tag{7}$$

The heavier the animal, the shorter its trunk relative to its width.

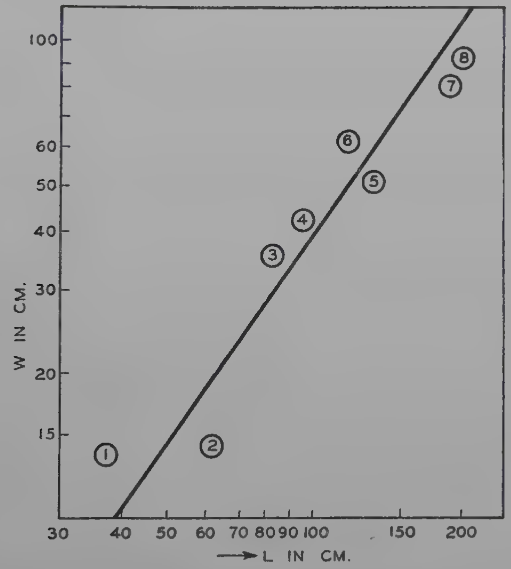

FIGURE 4. Width W of trunk plotted against length L of trunk on logarithmic scale. The straight line has the theoretically predicted slope 3/2. 1 — cat; 2 — dog; 3 — dog; 4 — goat; 5 — ass; 6 — saw; 7 — elk; 8 — ox. Data from Muybridge, (1887).

Of course we cannot expect such simple relations to hold exactly in reality. It is interesting, however, that to some degree of approximation the relation $W \propto L^{3/2}$ does actually hold, as seen from Figure 4, where W is plotted against L on logarithmic scale. We must however remember what has been said in the Introduction in regard to such agreements.

Similar crude considerations lead us to expect that the cross section of the legs will be roughly proportional to the mass M of the quadrupeds, since they have to be mechanically strong enough to support the body. Such an approximation is even cruder than the one made above about the trunk. The strength of the legs is determined not only by their role as "pillars" supporting the body, but by numerous other functions. The trend towards thicker legs in heavier animals is however unmistakable. Actual data are very scarce. To make even a rough comparison, the following procedure was used. Denoting the thickness of the extremities by d, its cross section is roughly d^2. We expect approximately $d^2 \propto M$, or because of relations (7), $d^2 \propto L^4$ or $d \propto L^2$. Hence $d/L \propto L$ or

$$d/L \propto M^{1/4}. \qquad (8)$$

The values of d/L were taken from pictures in volume 2 of the Anatomy of Vertebrates by R. Owen (1866); the values of M from tables compiled by G. Crile (1941, p. 284) and from C. Oppenheimer and L. Pincussen (1930, p. 732). The thickness of the femur was taken for d, the length between the shoulder blades and the pelvis for L. The vaules of d are extremely inaccurate. The results are plotted on Figure 5.

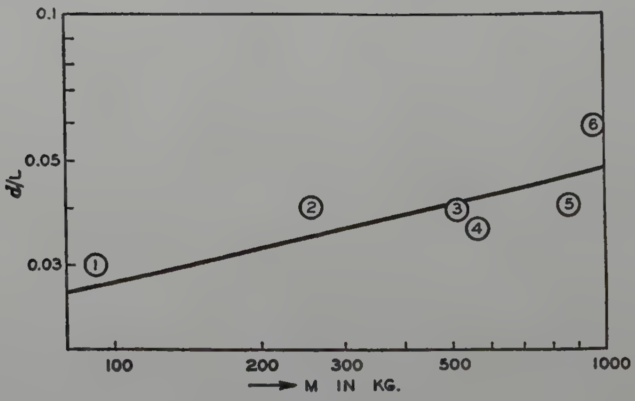

FIGURE 5. Ratio of thickness d of extremities to length L of trunk, plotted on logarithmic scale against mass M. The straight line has the theoretically predicted slope 1/4. 1 — lion; 2 — polar bear; 3 — horse; 4 — ox; 5 — giraffe; 6 — hippopotamus. For sources of data see text.

Thus from a purely theoretical point of view we see that the mass M *of a quadruped in principle may determine the size and shape of its trunk and the thickness of the extremities. This already specifies to a large extent its general form.*

In the next sections we shall see that an additional specification, namely the length of the extremities, may be obtained from considerations of locomotion.

It must be remarked that relations (7) determine L and W, and hence the surface of the animal in terms of M. Since Rubner's law requires that the total metabolism varies approximately as the surface of the body, this raises the question as to whether M and q may be considered as independent. However the surface of the extremities is not negligible as compared with that of the trunk, and therefore no definite conclusion can be drawn at this stage. Here is however a problem to be kept in mind.

IV. General Theory of Quadruped Locomotion

This problem shall also be treated in a very rough way. The idealized quadruped shall be assumed to be a bar of length L, supported on four extremities, all of the same length l. In order of decreasing simplicity we shall first discuss the case, when the extremities have no other joints, except those connecting them to the trunk. Subsequently we shall consider extremities with other joints. We shall neglect the lateral width of the trunk and the small lateral movement of the whole body, which results during the locomotion. Things will be considered to happen so, *as if* the trunk and extremities were infinitely thin. We shall also consider the simplest possible time sequence of the movements of the extremities, namely a rear and a front extremity move simultaneously forward or backward, remaining parallel. Whether the pair of simultaneously moving extremities is contralateral or collateral, is immaterial for our considerations because of the assumed infinite thinness of the body. The "idealized quadruped" has thus at any moment the shape represented on Figure 6.

The theory of any motion of such a system forms a part of the general dynamics of chains of linked levers. The general equations

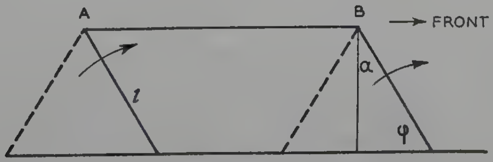

FIGURE 6

for such system have been developed by O. Fischer (1906). [C.f. also Winkelman and Grammel, 1927, p. 453]. Unfortunately, the non-linear differential equations involved are practically insoluble even in the simplest cases. While Fischer's theory in its general form, has been applied to some simple cases of systems of two levers only, it is at present of more interest from a mathematical point of view rather than from a biological. Some very drastic approximation method must be developed before the mathematical theory can be successfully applied to complex practical problems. Subsequently we shall suggest such an approximation method. For the present we must refrain from the mathematical rigour of the already developed theory of linked levers, and attempt to obtain specific, even though crudely approximate, results. The further development of the theory of animal locomotion depends however entirely on some practical approximation method to be adapted to O. Fischer's theory.

We shall make here a remark on the relation between biped and quadruped locomotion with rigid jointless extremities. It is readily seen that a biped could not have any locomotion at all in such a case. In order to impart a movement to the extremity *OB* (Figure 7) in the direction indicated by the arrow, the muscles, wherever their attachments may be, will tend to impart a movement to the "trunk" in the direction indicated by the arrow. In view of the rigidity of the triangle *OAB* , the trunk will rotate around *O* . Only if *OA* is not rigid, and can be bent, can it push the body forward by extension.

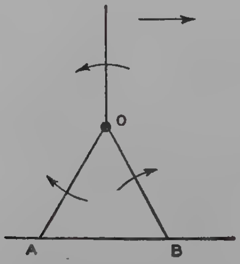

FIGURE 7

In case of a quadruped this difficulty does not exist. The imparting of a movement to the front extremity, as indicated by the arrow (Figure 6) tends to rotate the trunk counterclockwise around *B* , but this is opposed by the supporting action of the rear extremities. The counterclockwise motion around *A* , which tends to be produced by rotating the rear extremity as indicated by the arrow, is counteracted by the moment with respect to *A* of the force of gravity.

Running on extremities without middle joints. Using the notations of Figure 6, let the extremities which are extended forward be uniformly accelerated through the action of forces of constant moments in the direction indicated by the arrows. Put

$$d\phi/dt = \dot{\phi} = \omega \, . \tag{1}$$

The linear velocity v of the points A and B, and therefore of any point of the trunk is given by

$$v = l\omega \, . \tag{2}$$

The acceleration is equal to

$$v^2/l = l\omega^2 \, , \tag{3}$$

and if M is the mass of the whole system, we may approximately consider that per extremity the centrifugal force is equal to

$$\tfrac{1}{2} Ml\omega^2 \, . \tag{4}$$

Assuming that the other pair of extremities (Figure 6, broken lines) do not support the body during this phase of the locomotion, we find that the component of the force of gravity along l is

$$\tfrac{1}{2} M \, g \sin \phi \, , \tag{5}$$

where g is the acceleration constant.

When (4) becomes greater than (5), the system detaches itself from the ground. Hence at the moment when this happens, we have:

$$l\omega^2 = g \sin \phi \, . \tag{6}$$

Since $d^2\phi/dt^2 = \text{const} = a$, we have

$$\phi = \phi_0 + \omega_0 t + \tfrac{1}{2} at^2 \, , \tag{7}$$

where ϕ_0 and ω_0 are the initial values of ϕ and ω, for $t = 0$. Hence

$$\dot{\phi} = \omega = \omega_0 + at \, . \tag{8}$$

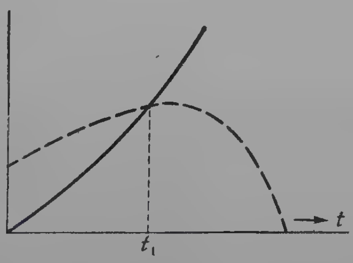

FIGURE 8

Introducing (7) and (8) into (6) we find:

$$l(\omega_0 + at)^2 = g \sin(\phi_0 + \omega_0 t + \tfrac{1}{2}at^2). \qquad (9)$$

The left side of (9) is represented by the full line in Figure 8, the right side by the broken line when $\omega_0 = 0$; $\phi_0 < \pi/2$, as usually will be the case. Then the lines intersect as shown in the Figure. In that case at the moment t_1 the system separates from the ground.

When the system has separated from the ground its center of gravity describes a parabola until an extremity again touches the ground. We thus have a sort of running, for running is defined as a locomotion, in which the animal is at times completely detached from the ground (Steinhausen, 1930, p. 220). Because of (3), equation (6) may be written:

$$v^2/l = g \sin \phi. \qquad (10)$$

The horizontal component of the velocity of the body is always less than v. Hence, for the average velocity $\overline{v}$ of running

$$\overline{v} < v. \qquad (11)$$

But from (10) it follows, that

$$v^2/lg < 1 \quad \text{or} \quad v^2 < l\,g. \qquad (12)$$

Hence *a fortiori*

$$\overline{v}^2 < lg; \overline{v} < \sqrt{lg}. \qquad (13)$$

With $l \backsim 100$ cm. we find

$$\overline{v} < 300 \text{ cm sec}^{-1}. \qquad (14)$$

With such a mechanism of running, a horse could not run faster than 3 meters per second, while smaller animals would run even much slower.

We may connect $\overline{v}$ with the average metabolic rate q erg. gm^{-1} sec^{-1}. While the system is still on the ground, we have:

$$\overline{v} = v \sin \phi; \sin \phi = \overline{v}/v. \qquad (15)$$

Equations (10) and (15) give

$$\overline{v} = v^3/gl. \qquad (16)$$

Neglecting the mass of the extremities as compared with that of the trunk, the kinetic energy which must be supplied to the system is approximately

$$\tfrac{1}{2}Mv^2.$$

When the system detaches itself from the ground, its center of gravity describes a parabola. The horizontal distance x which it covers until it reaches the same level above ground as it had at the moment of detachment is

$$x = (2v^2/g) \sin\phi \cos\phi \,. \tag{17}$$

The time it takes to cover that distance x is equal to $t = x/\bar{v}$. Hence from (17) and (15):

$$t = 2\, v \cos\phi/g \,. \tag{18}$$

We may consider t as the duration of each "running step". If all the kinetic energy $\frac{1}{2}\, M\, v^2$ is lost after each step, due to impact with the ground (which is the most unfavorable assumption), then the amount of energy supplied per second must be

$$\frac{Mv^2}{2\,t} = \frac{gMv}{4\cos\phi}. \tag{19}$$

This must be less than Mq. Hence, $\cos\phi$ being of the order of 1:

$$gv/4 \leqq q \quad \text{or} \quad v \leqq 4q/g \,. \tag{20}$$

Relations (16) and (20) now give

$$\bar{v} \leqq 64\, q^3/g^4 l \,. \tag{21}$$

With $q \backsim 10^5$ erg gm^{-1} sec^{-1}, and $l \backsim 10^2$ cm., we obtain $\bar{v} \leqq 10^3$ cm sec^{-1}. Hence from the point of view of energy supply this mechanism of running is adequate to give observed velocities. It is, however, inadequate from purely kinematic reasons, as we have seen above.

We may argue that the system detaches itself from the ground when the vertical component of the centrifugal acceleration $(v^2/l) \sin\phi$ exceeds the earth's acceleration g. This gives

$$v^2/l \sin\phi = g \,.$$

Substituting for v its expression (15), we find

$$\bar{v} \leqq \sqrt{gl \sin\phi}$$

which gives the same results as (13).

Thus far we have neglected the masses and the moments of inertia of the extremities. In the following we shall take them into consideration, and therefore shall derive here some simple relations.

Considering an extremity of length l and thickness b as a very oblong ellipsoid of revolution, we find for its moment of inertia I around an axis passing through the center of gravity

$$I = \frac{4}{120} \pi \rho l b^2 (\tfrac{1}{4} l^2 + \tfrac{1}{2} b^2) . \tag{22}$$

Let

$$b\sqrt{2}/l = \varepsilon ; \; 2b^2 = \varepsilon^2 l^2 . \tag{23}$$

Then

$$I = \frac{4}{960} \pi \rho \varepsilon^2 (1 + \varepsilon^2) l^5 . \tag{24}$$

Hence, putting

$$a = \frac{4}{960} \pi \rho \varepsilon^2 (1 + \varepsilon^2) \tag{25}$$

we have

$$I = a l^5 . \tag{26}$$

For similarly shaped extremities, their moments of inertia vary as the fifth power of their length.

With $\varepsilon \infty 10^{-1}$, $\rho \infty 1$, we have

$$a \infty 10^{-4} \text{ gm cm}^{-3} . \tag{27}$$

Walking on extremities without middle joints. Consider now a locomotion on jointless extremities in which the system does not detach itself from the ground, that is when a is so small, that t_1 in Figure 8 is to the right of the maximum of the broken line. This type of locomotion is usually called walking. We still assume the same symmetry condition for the movements of the rear and front extremities as before. During each step the trunk of mass M is lifted by the amount $l(1 - \cos \alpha)$, requiring an amount of work

$$Mgl(1 - \cos \alpha) . \tag{28}$$

Let the extremities swing with a constant average angular velocity ω. For the linear velocity of the trunk we have still the equation (2). The kinetic energy acquired by the trunk during each step is

$$\tfrac{1}{2} M v^2 = \tfrac{1}{2} M l^2 \omega^2 . \tag{29}$$

The kinetic energy acquired by each extremity is

$$I \omega^2 = a l^5 \omega^2 . \tag{30}$$

Hence, for all four extremities it is

$$4 a l^5 \omega^2 . \tag{31}$$

Let all of that energy be lost at the end of each step. If the forward moving extremity suddenly becomes fastened (through friction) to the ground upon contact, and the connection of the "propelling" extremity, which at the end of the step is directed backward, with the ground remains unsevered, such a total loss will happen, because we have at the end of a step a rigid triangular structure, fastened to the ground.

The total energy expenditure per step is

$$Mgl(1-\cos\alpha)+\tfrac{1}{2}Ml^2\omega^2+4al^5\omega^2. \tag{32}$$

The distance travelled during each step is

$$s=2l\sin\alpha\,. \tag{33}$$

While this distance is traveled, the extremity swings through an angle 2α with a uniform angular velocity ω. Hence the duration of each step is

$$t_s=2\alpha/\omega\,. \tag{34}$$

The average velocity during the step, which is the same as the average velocity of locomotion, is

$$\bar{v}=s/t_s=(l\omega\sin\alpha)/\alpha\,, \tag{35}$$

whence

$$\omega=\alpha\bar{v}/l\sin\alpha\,. \tag{36}$$

Substituting (36) into (32), the latter becomes

$$Mgl(1-\cos\alpha)+\tfrac{1}{2}M\frac{\alpha^2\,\bar{v}^2}{\sin^2\alpha}+\frac{4a\alpha^2\,l^3\,\bar{v}^2}{\sin^2\alpha}. \tag{37}$$

The total energy supply per step is

$$Mqt_s=\frac{2Mql\sin\alpha}{\bar{v}}, \tag{38}$$

because of (34) and (36).

Expression (37) must be less than or equal to (38). Hence

$$Mgl(1\cos\alpha)+\frac{1}{2}\frac{M\alpha^2\,\bar{v}^2}{\sin^2\alpha}+\frac{4a\alpha^2\,l^3\,\bar{v}^2}{\sin^2\alpha}\leqq\frac{2Mql\sin\alpha}{\bar{v}}. \tag{39}$$

The left side of (39), plotted as a function of l, is a cubic which becomes steeper with increasing $\bar{v}$ and also is displaced upwards as $\bar{v}$ increases (Figure 9,L). The right side is a straight line, the slope of which decreases with increasing $\bar{v}$. For sufficiently large values of $\bar{v}$, the two lines will not intersect, and relation (39) is impossible.

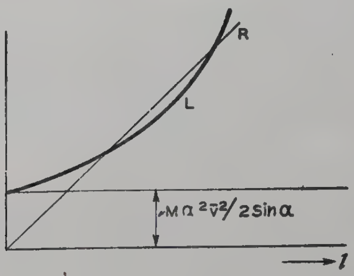

FIGURE 9

The upper limit of $\vec{v}$, for which the equality of (39) just holds, can be found in the following way. When $\vec{v}$ has its highest possible value, $\bar{v}_m$, the lines L and R are tangent. Hence

$$Mg(1-\cos\alpha)+\frac{12\,a\alpha^2\,l^2\,\bar{v}_m{}^2}{\sin^2\alpha}=\frac{2\,Mq\sin\alpha}{\bar{v}_m}.$$

In order that this equation should have a real root we must have

$$(2\,Mq\sin\alpha)/\vec{v}_m-Mg(1-\cos\alpha)>0$$

or

$$\vec{v}_m<(2\,q\sin\alpha)/g(1-\cos\alpha). \tag{40}$$

For $\alpha=\pi/2$, $(\sin\alpha)/(1-\cos\alpha)=1$. For $\alpha\rightarrow 0$ it tends to ∞ as $2/\alpha$. Hence we can have as high a $\bar{v}_m$ as we wish by taking sufficiently small values for α. For small α's (40) gives

$$\bar{v}_m=4\,q/g\,\alpha;\ \alpha=4\,q/g\,\bar{v}_m. \tag{41}$$

With $q\backsim 10^5$ erg gm^{-1} sec^{-1}, in order to obtain $\bar{v}_m\backsim 10^3$ cm sec^{-1} we must have

$$\alpha=10^{-1}\backsim 6^\circ. \tag{42}$$

Equation (36) gives for small values of α

$$\omega\backsim\bar{v}/l. \tag{43}$$

With $l\backsim 10^2$ cm we find $\omega\backsim 10$ sec^{-1}, and therefore from (34)

$$t_s\backsim 10^{-2}\text{ sec}.$$

The frequency of steps should be about 100 per second, while the length of the step is found from (33) to be $s=2l\alpha\backsim 10$ cm. With $l\backsim 10$ cm we have $\omega\backsim 10^2$ sec^{-1}; $t_s\backsim 10^3$ sec, $s\backsim 1$ cm.

Contrary to the process of running, discussed above, walking on jointless extremities is not limited by any kinematic considerations. It is not limited by considerations of energy supply, either. However, in order to obtain plausible values of the velocities of locomotion, it is necessary to have such high frequencies of steps, that two new limiting factors will enter. One is the inertia of the extremity. With frequencies of the order of 100 sec^{-1}, the acceleration will be so high, that normal muscular forces will not be able to produce them, unless we limit ourselves to very small organisms with small masses, like insects, to which the above considerations do not apply anyway. Another limiting factor is the muscular viscosity (A. V. Hill, 1927); which again will prevent displacements of large muscular masses with such frequencies.

All in all, *the above considerations indicate the reasons of inadequacy of jointless extremities for quadruped locomotion, and throw some light on the reasons why animals with such extremities do not occur.*

Running on extremities with one or more middle joints. Now let us consider a different type of running, when the extremities have one or more middle joints. By folding and unfolding the extremities, the animal may repel the body from the ground in any definite direction. The necessity of considering four extremities, discussed on page 18, now does not exist, and we may simplify our considerations, by considering the dynamics of two extremities only. The locomotion of a quadruped may now be considered as a locomotion of "two bipeds connected in series".

Let the repelling action of an extremity impart to the center of gravity of the body a velocity v, forming an angle ϕ with the horizontal, and cause the system to be detached from the ground. The center of gravity then describes a parabola, and the horizontal distance traveled by the center of gravity until it reaches the same horizontal level is

$$x_h = (2\, v^2/g) \sin\phi \cos\phi \,. \tag{44}$$

The time it takes to cover that distance is

$$t_0 = x_h/v \cos\phi = (2\, v \sin\phi)/g \,. \tag{45}$$

If we neglect for the time being, the length of the extremity, then t_0 is essentially the duration of the step, while

$$\bar{v} = v \cos\phi \,, \tag{46}$$

is the speed of running.

The energy available per step is

$$Mq\,t_0 = (2\,Mq\,\bar{v}\tan\phi)/g\,. \tag{47}$$

The total energy imparted to the body, neglecting the work of the necessary lift during the "unfolding" of the extremity, is $\frac{1}{2}Mv^2$. Not all of the energy is lost at the end of the step. If the forward swinging extremity hits the ground at an angle $\pi/2$, then approximately only the vertical component of the velocity v is lost. The amount of energy lost is then, because of (46):

$$\tfrac{1}{2}M\,v^2\sin^2\phi = \tfrac{1}{2}M\,\bar{v}^2\tan^2\phi\,. \tag{48}$$

This must be equal to or less than (47). Hence

$$\bar{v} \leqq 4\,q/g\,\tan\phi\,. \tag{49}$$

If with $q \sim 10^5$ erg gm^{-1} sec^{-1} we wish to have $\bar{v} \sim 10^3$ cm sec^{-1}, we must take $\tan\phi \sim 0{\cdot}3$ or $\phi \sim 15°$. It is noteworthy, that examining photographic pictures of galloping horses, cats, dogs, etc. (Muybridge, 1887), we find in many cases, that during the "flight phase", when the animal is completely detached from the ground, the angle formed by the extremities with the ground is of that order of magnitude.

Several improvements can be made in the above reasoning. First of all we should bring into consideration the length of the extremities, which does not enter into equation (49). We shall subsequently introduce the length of the extremities by considering the muscular force necessary to impart motion to the body. But quite apart from any such considerations, the length of the extremities may be introduced in the following manner.

Let the forward swinging extremity hit the ground in such a position, that the line OA (Figure 10) is vertical, so that approximately only the vertical component $v\sin\phi$ of the velocity is lost. Then the horizontal velocity $\bar{v}$ remains the same, and as the extremity now unfolds, it communicates to the body the lost vertical momen-

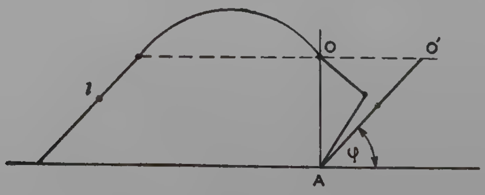

FIGURE 10

tum, which is regained when the extremity is in the "unfolded" position AO'. During this period the body moved the distance $OO' = l \cos \phi$, and this takes a time

$$t_1 = l \cos \phi / v \cos \phi = l/v\,. \tag{50}$$

Hence the total duration of the "step" is, because of (45):

$$t_0 + t_1 = \frac{2\,v \sin \phi}{g} + \frac{l}{v}, \tag{51}$$

and the energy available per step is now

$$\frac{2\,v\,Mq \sin \phi}{g} + \frac{Mq\,l}{v} = \frac{2\,Mq\,\bar{v} \tan \phi}{g} + \frac{Mq\,l \cos \phi}{\bar{v}}. \tag{52}$$

Setting this equal to or greater than (48), we now have:

$$\tfrac{1}{2}\,\bar{v}^2 \tan^2 \phi \leqq \frac{2\,q\,\bar{v} \tan \phi}{g} + \frac{ql \cos \phi}{\bar{v}}, \tag{53}$$

which, for the case of equality is a cubic equation in $\bar{v}$, and expresses $\bar{v}$ as a function of l. The value of $\bar{v}$ obtained from (53) is higher than the value obtained from (49). That value increases with increasing l.

We have neglected so far the mass of the extremities as compared with that of the body. In most cases, except in man, this is probably justified for a rough approximation.

If the extremity which swings forward hits the ground not when perpendicular to it, then part of the horizontal component $v \cos \phi$ of the velocity will also be lost. If we assume that all of the kinetic energy is lost at the end of each step, then we have, by requiring now that (47) be greater than or equal to $\tfrac{1}{2}Mv^2$:

$$\tfrac{1}{2}Mv^2 \leqq (2\,Mq\,\bar{v} \tan \phi)/g\,, \tag{54}$$

or

$$\bar{v} \leqq \frac{4\,q \tan \phi \cos^2 \phi}{g}, \tag{55}$$

which gives the same order of magnitude as (49).

The work of lifting the body during the process of unfolding the extremity is also in general of the same order of magnitude as the kinetic energy $\tfrac{1}{2}Mv^2$ and its introduction does not alter the situation appreciably.

The fundamental difference between this mechanism of running and the one discussed above for rigid extremities, is that in the former case the duration of the step decreases with increasing $\bar{v}$, while in the latter case that duration increases with $\bar{v}$. This is seen for the former case by combining (34) and (36), which gives

$$t_s = (2\,l \cos\phi)/\bar{v}\,.$$

For the latter it follows from (45). Thus with folding extremities, the higher $\vec{v}$, the higher the amount of energy available per step.

Muscular forces in running. All the above discussions apply to continuous running and take into consideration only the continuously available supply of energy. Now we shall consider the problem from another angle, namely from the point of view of the mechanical forces available to produce the necessary accelerations.

First consider the case of walking on rigid extremities, whose mass we again shall neglect. The length of each step is given by (33), while the duration is equal to $t_0 = (2l \sin\alpha)/\bar{v}$. The angular velocity is given by (36). Hence the average total linear velocity is

$$v = l\,\omega = \alpha\,\bar{v}/\sin\alpha\,.$$

Since that average velocity is reached approximately within a time $\frac{1}{2}\,t_0$, beginning with zero velocity, the average acceleration is

$$\dot{v} = 2v/t_0 = \alpha\,\bar{v}^2/l\,\sin^2\alpha\,. \tag{56}$$

Hence the average force is

$$M\,\alpha\,\vec{v}^2/l\,\sin^2\alpha\,. \tag{57}$$

This force is supplied by the muscles of the extremity and is approximately proportional to their cross-section, other conditions being equal (A. V. Hill, 1927). The muscular force is opposed by the weight of the body which is equal to Mg. Denoting by s the average thickness of the extremity and by f a coefficient of proportionality, the total force is equal to

$$fs^2 - Mg\,. \tag{58}$$

Equating (57) to (58) we obtain

$$\bar{v} = \sqrt{\frac{(fs^2 - Mg)\,l}{M\alpha}}\,\sin\alpha. \tag{59}$$

The force exerted by a muscle is of the order of 10 Kg cm^{-2} ∞ 10^7 dyne cm^{-2}. Hence $f \infty 10^7$ dyn cm^{-2}. With $\sin\alpha \infty 1$, $\alpha \infty 1$; $s \infty 10$ cm, $M \infty 10^5$ gm; $l \infty 10^2$ cm; we find $Mg \infty 0{\cdot}1\,fs^2$. Thus the Mg

term may be neglected, and equation (59) gives $v \backsim 10^3$ cm sec^{-1}.

A sustained velocity of that magnitude will not be possible, however, because for $q \backsim 10^5$ erg gm^{-1} sec^{-1} we must have much smaller values of α and $\sin \alpha$, as we have seen in discussing expression (41).

In the case of running with non-rigid extremities we have for the duration of the action of the force the value t_1 given by (50). Since, to a first approximation, only the vertical component of v is affected in that case, we see that during the time l/v the velocity changes from 0 to $v \sin \phi$. Hence, the average acceleration is $v^2 \sin \phi / l$ and the average v force is $Mv^2 \sin \phi / l$. Putting this equal to $fs^2 - Mg$, and remembering (46) we find

$$\bar{v} = \sqrt{\frac{(fs^2 - Mg)l}{M \sin \phi}} \cos \phi, \tag{60}$$

which is similar to (59). For $\phi \backsim 15°$, which, as we have seen, (p. 26) is needed for a sustained velocity, we find $\cos \phi / \sqrt{\sin \phi} \backsim 1{\cdot}7$, and thus *with non-rigid extremities velocities of* 10^3 cm sec^{-1} *may be sustained continuously both from the point of view of energy supply as well as from the point of view of muscular forces available.*

Equation (60) may be written

$$\bar{v} = \sqrt{\frac{fs^2\, l}{M \sin \phi} - \frac{gl}{\sin \phi}} \cos \phi. \tag{61}$$

The quantity $s^2 l$ is the volume of the extremity, which is roughly proportional to its mass. Hence for similarly built animals $s^2 l / m = \gamma =$ const. If the second term is small, as compared with the first, which as we have seen is the case, then

$$\bar{v} = \sqrt{\frac{f\gamma}{\sin \phi}} \cos \phi. \tag{62}$$

Hence, *for similarly built animals the maximum velocity is independent of the size of the animal, other physicochemical conditions (which enter in* f*) being the same.* This result has been previously obtained in a different way by A. V. Hill (1927).

On the other hand, if we assume, as in section *III*, that s^2 is proportional to M, so that, denoting by k a constant $s^2 = kM$, then, again neglecting the term in g:

$$\bar{v} = \sqrt{\frac{f k l}{\sin \phi}}. \tag{63}$$

The velocity now is independent on the mass of the animal, but proportional to the square root of the length of the extremities. Similar relations have been derived previously from purely dimensional considerations involving some doubtful assumptions (Thompson, 1942). A comparison of such a relation with observations presents great difficulties in view of the scarcity of data. Hitherto almost the only available data on the speed of animals are given by the series of instantaneous photographic pictures published by E. Muybridge (1887). They give interesting insight into different modes of locomotion, such as walking, trotting, galloping. In no case do we have the certainty that the *maximum* speed has been observed in any of the locomotions. For comparison with equation (63) we must choose the speediest form of locomotion—galloping. A few data could thus be found in Muybridge's publication, and they are represented on Figure 11. For a greyhound the observed velocity is however much too high.

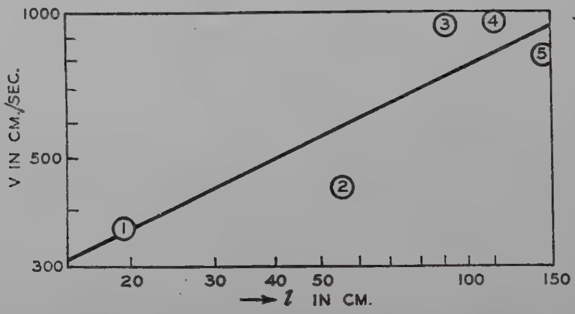

FIGURE 11. Velocity v of galloping plotted against length l of extremities on logarithmic scale. The straight line has the theoretically required slope 1/2. 1 — cat; 2 — goat; 3 — elk; 4 — horse; 5 — camel. Data from Muybridge (1887).

It would certainly be of interest to obtain more detailed data on various animals by means of a cinema film. The quantity f could in principle be measured on each animal and the cross-section s^2 can also be directly determined. Thus it would be possible to directly compare equation (60) with observations.

Before any worth-while discussion of the available data can be made, the theory will have to be considerably improved. Instead of using average velocities and accelerations, it will be necessary to establish more exact, although still approximate, equations of motion for the folding and unfolding of an extremity. The relative dimensions of each part of the extremity, in other words, *the location of the middle joint,* may then be determined by the requirement of a maximum possible velocity, considered as a function of those dimensions. The next extension would be to determine from similar considerations *the optimum number of joints.* Besides considerations of locomotion, other considerations will enter into that problem. An extremity ending in a thin stump would be of little use on a soft ground. This alone, regardless of other reasons may require an extra joint, forming the foot.

A more detailed study of the losses of the energy due to impact against the ground, will also have to be studied. This also will contribute to the determination of the structure, and hence of the shape of the extremities. An approach in that direction is made in section *V*.

The requirements of maximum *short time velocity* or of maximum acceleration are different from those of sustained running. The study of this aspect of locomotion will lead into a theory of jumping and require considerations of *extremities of unequal length.* Even the role of an additional extremity in jumping—the tail, may be brought quantitatively into those studies. All such studies will determine more closely the external shape of the animal. But even with the present crude approximation we have the following result.

For a given mass of the animal, the size and shape of its trunk are determined by relations (7) *of section III, while the thickness of the extremities is determined by relation* (8) *of that section, the length of the extremities is given by equation* (60) *of this section. The general outside shape of the animal is thus determined quantitatively to quite a large extent even by those simple considerations.*

In addition to that it may readily be seen that the total length of the neck must be of the order of magnitude of the length of the extremities, in order that the animal could reach food on the ground. The thickness of the neck will be determined for a given length, by the weight of the head. The latter in its turn is approximately proportional to the weight of the brain. It is empirically known (Crile, 1941, p. 210), that the brain weight of animals is approximately proportional to the total metabolism*) qM . *Hence,* q *and* M *determine, together with the shape of the trunk and the thickness and length of extremities also, the size of the head and the length and width of the neck.*

With the exception of the tail, we thus have a fairly complete description of the general shape of a quadruped in quantitative terms.

The approximate proportionality of the weight of the brain and of qM still awaits a theoretical explanation. Perhaps it may be found through the consideration that the more complex a brain, the larger the number of innervated muscle fibers and other end organ units, the tonic activity of which consumes energy.

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* Crile does not give the source of his data for q , and we feel therefore, that the above relation must be taken with due reservation.

The above mentioned linear relation between qM and the weight of the brain makes it rather pointless to assume, as we have done previously (Rashevsky, 1943a), that the brain weight is to be considered as an independent determining parameter. It also makes untenable the previously suggested hypothesis, that the degree of nervous coordination available is responsible for the use of two rather than four extremities for walking and running (Rashevsky, 1943a). The reasons why most animals use four extremities for locomotion, when two seem to be sufficient, must be sought elsewhere, and may well lie in some details, as yet not studied, of the dynamics of locomotion.

As regards arthropods the larger number of extremities in those animals will likely be explained by the "relative roughness" of the ground (Rashevsky, 1943a; p. 40) and other similar considerations. The locomotion of jumping insects, like fleas or grasshoppers is more aptly described as biped.

All the above holds on the assumption of the constancy of other parameters, in particular of f. The latter is largely determined by the physicochemical constituents of the animal. It may well happen that f may itself be considered as an independent determining parameter of the organism. This does not alter anything in the general situation. We determine the shape of the organism in terms of continuously varying biological parameters, which describe the physicochemical constitution and the physiological functions of the organisms.

V. Loss of Energy Due to Impact of Extremity Against the Ground

In this section we shall study a few of the simplest cases of the problem. Further extensions of this investigation will be evident.

Let us compute the loss of energy, due to impact against the ground of an extremity, without knee-joint, directed forward. Let us first neglect the mass of the extremity. Let (Figure 12) the center of the gravity of the whole system be at S_0, the middle of the line

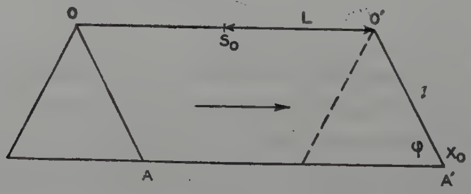


FIGURE 12

OO', of length $2L$. Let the coordinates of S_0 be x and y, and the velocity components just before the impact be

$$\dot{x}_0 = v > 0 ; \; \dot{y}_0 = -w < 0 . \tag{1}$$

After the impact, which is supposed to take place simultaneously with the front and rear extremity, so that $OA \parallel O'A'$ and OO' is horizontal, we have, denoting by x_0 the abscissa of the point of impact A', which after the impact remains fixed:

$$(x_0 - L - x)^2 + y^2 - l^2 = 0 , \tag{2}$$

or, putting

$$x_0 - L = \bar{x} ,$$

$$(\bar{x} - x)^2 + y^2 - l^2 = 0 . \tag{3}$$

We shall apply the Lagrangian equation for the calculation of values of $\dot{x}$ and $\dot{y}$ after the impact (Appell, 1924, p. 531). To this end we introduce new variables

$$q_1 = x ; \; q_2{}^2 = (\bar{x} - x)^2 + y^2 - l^2 . \tag{4}$$

Due to the constraint (3) introduced by the impact, we have at the moment of impact and at all times thereafter

$$q_2 = 0 . \tag{5}$$

Denote by T the kinetic energy of the system

$$T = \tfrac{1}{2} M (\dot{x}^2 + \dot{y}^2) . \tag{6}$$

By making the substitution (4), T becomes a function of q_1, q_2, $\dot{q}_1$ and $\dot{q}_2$. We now have, denoting by the superscript 0 the values just before the impact, and by the asterisk the values just after the impact:

$$\left(\frac{\partial T}{\partial \dot{q}_1} \right)^{*} - \left(\frac{\partial T}{\partial \dot{q}_1} \right)^{0} = 0 . \tag{7}$$

From (4) we have

$$y^2 = q_2{}^2 + l^2 - (\bar{x} - x)^2 . \tag{8}$$

Differentiating, dividing by $2y$, squaring and again using (8), we find:

$$\dot{y}^2 = \frac{q_2{}^2 \dot{q}_2{}^2 + (\bar{x} - q_1)^2 \dot{q}_1{}^2 + 2 q_2 \dot{q}_2 (\bar{x}_0 - q_1) \dot{q}_1}{q_2{}^2 + l^2 - (\bar{x} - q_1)^2} . \tag{9}$$

Introducing (9) into (6), we find, remembering that, because of (4), $\dot{x} = \dot{q}_1$,

$$T = \tfrac{1}{2}M\left[\dot{q}_1^2 + \frac{q_2^2\dot{q}_2^2 + (\bar{x} - q_1)^2\dot{q}_1^2 + 2q_2\dot{q}_2(\bar{x}_0 - q_1)\dot{q}_1}{q_2^2 + l^2 - (\bar{x} - q_1)^2}\right]. \quad (10)$$

Hence

$$\frac{\partial T}{\partial \dot{q}_1} = M\dot{q}_1 + \frac{M(\bar{x} - q_1)^2\dot{q}_1 + Mq_2\dot{q}_2(\bar{x}_0 - q_1)}{q_2^2 + l^2 - (\bar{x} - q_1)^2}. \quad (11)$$

To obtain $(\partial T/\partial \dot{q}_1)^*$ and $(\partial T/\partial \dot{q}_1)^0$ we must substitute into (11) the values which q_1, $\dot{q}_1$, q_2 and $\dot{q}_2$ have just after and before the impact, correspondingly. We shall denote those values with an asterisk and a superscript ^{0} respectively. But $\dot{q}_2^{*2}$ is zero, because $\dot{q}_2^*$ becomes zero at the moment of impact and remains zero thereafter. Keeping this in mind, as well as the fact that the denominator of (11) does not change during the impact and is equal to $l^2 \sin^2 \phi_0$, where ϕ_0 is the value of ϕ at the moment of impact, we have:

$$\left(\frac{\partial T}{\partial \dot{q}_1}\right)^* - \left(\frac{\partial T}{\partial \dot{q}_1}\right)^0 = M(\dot{q}_1^* - \dot{q}_1^0) + \frac{M(\bar{x} - q_1^0)^2(\dot{q}_1^* - \dot{q}_1^0) - Mq_2^0\dot{q}_2^0(\bar{x} - q_1^0)}{l^2 \sin^2 \phi_0}. \quad (12)$$

Now we may substitute into (12) the original variables x and y. We notice that

$$\dot{q}_1^* - \dot{q}_1^0 = \dot{x}^* - \dot{x}^0 = v^* - v^0; \; (\bar{x} - q_1^0) = l\cos\phi_0. \quad (13)$$

The value of $q_2^0\dot{q}_2^0$ just before the impact is otained from (4). Differentiating with respect to t, we find that before the impact:

$$q_2\dot{q}_2 = y\dot{y} - (\bar{x} - x)\dot{x}. \quad (14)$$

but at the moment just before the impact, $\bar{x} - x = l\cos\phi_0$, $y = l\sin\phi_0$, $\dot{x} = v$, $y = -w$. Hence

$$q_2^0\dot{q}_2^0 = -l(v\cos\phi_0 + w\sin\phi_0). \quad (15)$$

Equation (15) shows, that, since at the moment of impact q_2^0 becomes zero, $\dot{q}_2^0$ becomes negatively infinite. This is obvious, since the velocity changes discontinuously.

Introducing (15) and (13) into (12), and the latter into (7) we find, after rearranging:

$$v^* - v = -\cos\phi_0 (v\cos\phi_0 + w\sin\phi_0) < 0 . \qquad (16)$$

The expression in parentheses is the projection $\mathfrak{v}_l$ on l of the total velocity $\mathfrak{v}$ of the center of gravity. Hence the loss of the horizontal component of $\mathfrak{v}$ is equal to the horizontal component of $\mathfrak{v}_l$.

Solving (3) for y^2 and differentiating with respect to t , we find, remembering (13):

$$\dot{y}^* = \frac{\bar{x}_0 - x^*}{y^*}\dot{x}^* = \dot{x}^* \operatorname{ctn}\phi_0 . \qquad (17)$$

To compute the total loss in kinetic energy due to the impact, we remember that

$$T^* = \tfrac{1}{2}M(\dot{x}^{*2} + \dot{y}^{*2}) ; \; T^0 = \tfrac{1}{2}M(v^2 + w^2). \qquad (18)$$

Hence

$$T^0 - T^* = \tfrac{1}{2}M(v^2 + w^2 - \dot{x}^{*2} - \dot{y}^{*2}). \qquad (19)$$

Solving equation (16) for v^* , introducing it into (17) and then introducing v^* and (17) into (19), we obtain after rearrangements,

$$\Delta T = T^0 - T^* = \tfrac{1}{2}M(v\cos\phi_0 + w\sin\phi_0)^2 = \tfrac{1}{2}M\mathfrak{v}_l^2 . \qquad (20)$$

Thus *the total loss of kinetic energy is equal to the kinetic energy of a system, having a velocity equal to the projection on* l *of the actual velocity of the system.*

ΔT becomes equal to $\frac{1}{2}M(v^2 + w^2) = T^0$, that is all kinetic energy is lost, if $\mathfrak{v}$ coincides with $\mathfrak{v}_l$, that is if

$$\frac{w}{v} = \tan\phi_0 ; \; w = v\tan\phi_0 . \qquad (21)$$

ΔT is zero, when

$$\tan\phi_0 = -\frac{v}{w} , \qquad (22)$$

that is, when $\mathfrak{v}$ is perpendicular to l .

If the center of gravity moves before the impact only under the influence of gravity, having at the moment $t = 0$ the coordinates $x = x_1$ and $y = h$ and the velocity component $\dot{x} = v$ and $\dot{y} = 0$, thus describing a parabola, then we have

$$x = vt ; \; y = h - \tfrac{1}{2}gt^2 . \qquad (23)$$

At the moment of impact t_0 , $y = l\sin\phi_0$. Hence

$$h - \tfrac{1}{2}gt_0^2 = l \sin \phi_0$$

or

$$t_0 = \sqrt{\frac{2h - 2l \sin \phi_0}{g}}. \tag{24}$$

The velocity $\dot{y}$ is equal to $-gt$, and therefore at t_0 it is equal to

$$-w = -gt_0 = -\sqrt{2g(h - l \sin \phi_0)}\ (< 0). \tag{25}$$

Introducting this into (20) we find

$$\Delta T = \tfrac{1}{2}M(v \cos \phi_0 + \sqrt{2g(h - l \sin \phi_0)} \sin \phi_0). \tag{26}$$

In particular we may consider the following case. Let the system be propelled to the right by the rotation of the extremities clockwise. Consider that at the moment when $\phi = \pi/2$, and S is at its highest position, the lower end of the extremity becomes disconnected with the ground, sliding on the latter without friction. Then S will move on a parabola, its coordinates being given by (23). The extremity, paired to the propelling one, is swinging forward. We assume that it also drags on the ground without friction, until its angle ϕ becomes equal to ϕ_0. Then it suddenly becomes attached to the ground. A similar situation will arise, if, in order to avoid rubbing the ground with the forward swinging extremity, the body is slightly swayed to the side opposite to that extremity. When $\phi = \phi_0$, then the body weight is applied to it in full.

We now have $h = l$, and (26) gives

$$\Delta T = \tfrac{1}{2}M(v \cos \phi_0 + \sqrt{2l\,g(1 - \sin \phi_0)} \sin \phi_0). \tag{27}$$

$\Delta T = 0$ for $\phi_0 = \pi/2$. The loss ΔT is the less, the smaller the "steps".

If we take into consideration the mass of the extremities, the expressions become more complicated.

VI. Suggestions for an Approximation Method for Solving the Equations of Motion of a Chain of Linked Levers

The equations in question are of the form (O. Fischer, 1906; Winkelman and Grammel, 1927)

$$a_0\ddot{\phi}_i + \sum_k a_k(\ddot{\phi}_k + \dot{\phi}_k^2)\, f(\phi_i - \phi_k) = u(\phi_i), \tag{1}$$

where ϕ_i are the angles determining the positions of the individual levers of the chain, f and u are continuous functions, and a_k are constants.

Let during the interval $0 - t_1$ the average values of $\dot{\phi}_i$ be $\bar{\dot{\phi}}_i$.

Then the average values of ϕ_i at the moment t_1 are $\bar{\phi}_i = \frac{1}{2}\,\bar{\dot{\phi}}_i\, t_1$. The average accelerations are $\bar{\ddot{\phi}} = \bar{\dot{\phi}}/t_1$. Substituting those averages into (1), we have

$$a_0\, \bar{\dot{\phi}}/t_1 + \sum_k a_k(\bar{\dot{\phi}}_k/t_1 + \bar{\dot{\phi}}_k^2)\, f(\tfrac{1}{2}\bar{\dot{\phi}}_i t_1 - \tfrac{1}{2}\bar{\dot{\phi}}_k t_1) = u(\bar{\dot{\phi}}_i\, t_1)\,. \qquad (2)$$

These are algebraic equations, which determine the values $\bar{\dot{\phi}}_i$ as functions of t_1.

If at $t = 0$, $\dot{\phi}_i = \dot{\phi}_{0i} \gtrless 0$, then we put for $t = t_1$:

$$\bar{\phi}_i = \frac{\dot{\phi}_{0i} + \bar{\dot{\phi}}_i}{2}\, t_1\,,\ \bar{\ddot{\phi}}_i = \frac{\bar{\dot{\phi}}_i - \bar{\dot{\phi}}_{0i}}{t_1}. \qquad (3)$$

Substituting (3) into (1) we again obtain algebraic equations, expressing $\bar{\dot{\phi}}_i$ in terms of t_1 and ϕ_{0i}.

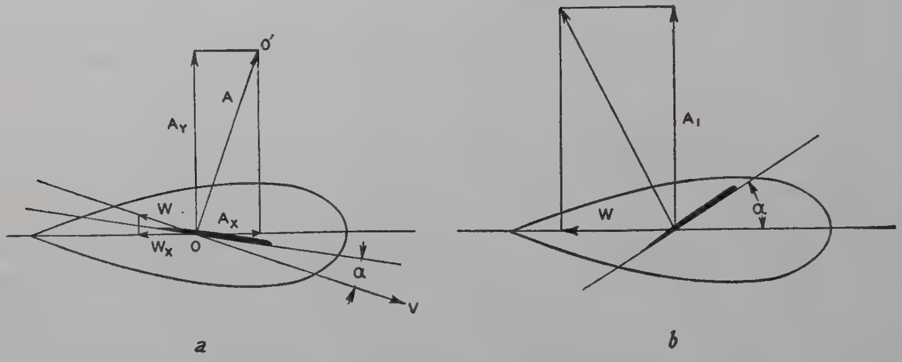
This method may work if the velocities and accelerations are monotonic functions of t in the interval 0, t_1 and if the accelerations do not vary too rapidly in that interval.

VII. Flight of Birds and Insects in Relation to Their Form

Even a remotely exact theory of flight of birds and insects meets with almost insuperable difficulties at present. In fact the relatively simpler problems of aircraft design are still based on semi-empirical foundations, since a complete synthetic theory of aerodynamics is still wanting. The relative simplification of the problems of aircraft engineering is due partly to the circumstance, that the two principal types of aerodynamical structures involved are the ordinary wing and the propeller. The action of both involves to a large extent stationary aerodynamical states, when continuous operation is considered. The situation with birds is different. While the wing represents an aerodynamical profile, yet its movement through air is anything but stationary. Inertial forces due to acceleration, which do not enter into the theory of the airplane wing, probably play here a very important role.

From studies by Marey (1893) and from pictures by E. Muybridge (1887) one gets the following general impression of the mechanism of the flight of a bird.

During the downstroke, (Figure 13a) the wing moves down and forward, with the velocity v. The lift A has thus a component directed forward (A_x). The resistance W has a horizontal component W_x directed backward. Apparently $A_x - W_x > 0$, and causes the bird to move forward. The vertical components $A_y + W_y$ compensate at least partly for the force of gravity Mg, M being the mass of the bird, g the acceleration of gravity. Actually $A_y + W_y$ is less than Mg, because, according to Marey, during the downstroke the bird looses slightly in altitude.



FIGURES 13*a* AND 13*b*

During the upstroke the wings move backwards and upwards much more slowly than during the downstroke. The bird moves forward, due to the momentum imparted previously by $A_x - W_x$, with a velocity v_1 (Figure 13b), which gradually decreases due to resistance. Because of a larger angle of attack α, the lift A_1, which is now directed vertically, is greater than A_y before, so that $A_1 > Mg > A_y$, and the bird again gains altitude.

While in a sense the wing acts as an aerodynamic profile both during the downstroke and during the upward stroke, yet in no case can the ordinary theory of an airplane wing be applied with any accuracy. For neither the velocity v in Figure 13a, nor v_1 in Figure 13b are uniform. Nor is the direction of the velocity with respect to the wing constant. In fact in both cases the tip of the wing has a much higher velocity than the point of attachment which remains stationary with respect to the body of the bird. This suggests that the wing may be acting as a propeller blade (Pettigrew, 1875; cited from M. H. Fischer, 1930, p. 340), rotating approximately around the axis OO' (Figure 13a) and propelling itself in that direction. The vertical component then provides for the maintenance of altitude, the horizontal—for the forward movement. But again the fundamental difference between a theory of such an action and that of a propeller is that the former does not correspond to a stationary state of rotation. Moreover the two wings must be considered as two propeller blades moving in opposite directions and their mutual disturbance will be very complex. Thus we have in a bird a new type of aerodynamic lifting surface, which is neither a stationary moving wing nor a propeller, but a system *sui generis*, the theory of which must still be developed.

From Marey's studies it appears that the flight of insects is based on a somewhat similar mechanism.

At the end we shall suggest a rough, but somewhat detailed analysis of the above discussed process of flight. Now we shall confine ourselves to very rough and general approximations, based largely on dimensional considerations.

Whatever the details of the actual mechanism may be, we may consider that the total velocity of locomotion $\vec{v}$ of the animal through air is less than, but of the same order of magnitude as the velocity v of the wing through air. Thus

$$\bar{v} \infty v \,. \tag{1}$$

Denoting by L the length of a wing and by S its width, by ρ the density of air ($\rho = 1{\cdot}2 \times 10^{-3}$ gm cm^{-3}) and by c_a and c_w the lift and resistance coefficients of the wing, we find for the force of resistance, F_r, approximately

$$F_r = \tfrac{1}{2}\, c_w \,\rho L S\, v^2 \,. \tag{2}$$

If the frequency of wing movements is ν, then the average velocity v is

$$v \infty L\nu \,. \tag{3}$$

Since this velocity v is acquired approximately during a time $1/\nu$, the average acceleration is

$$\bar{\dot{v}} \infty L\,\nu^2 \,. \tag{4}$$

If we put the density of the wing equal to ρ', and its average thickness to Δ, we have for its mass M_w:

$$M_w \infty L S \rho' \Delta \,. \tag{5}$$

Hence the average inertial force is

$$F_i = M_w \bar{\dot{v}} \infty L^2 S\, \nu^2\, \Delta\, \rho' \,. \tag{6}$$

The total force $F_i + F_r$ must be exercised by the body in order to move the wing with the desired velocity. This muscular force may be put as proportional to $M^{2/3}$, since it is proportional to the cross section of the muscles. Hence we have from (2) and (6), denoting by a'_1 and f two coefficients:

$$a'_1\, L^2 S \Delta v^2 \rho' + \tfrac{1}{2}\, c_w \rho L S\, v^2 \propto f\, M^{2/3}, \tag{7}$$

or, because of (3), with a_1 as a new coefficient and remembering that there are two wings, so that F_r must be doubled:

$$a_1\, S\Delta\, \rho'\, v^2 + c_w \rho L S\, v^2 \propto f\, M^{2/3}\,. \tag{8}$$

The lifting force of the two wings is equal to $c_a \rho L S\; v^2$ and this must be equal to Mg. Hence

$$LS \propto \frac{Mg}{c_a\, \rho\, v^2}. \tag{9}$$

Solving (8) and (9) for L and S, we find: with $\varepsilon = c_w/c_a$:

$$L \propto \frac{a_1\, M\, \Delta\, g\, \rho'}{c_a \rho\, (f M^{2/3} - \varepsilon\, Mg)} = \frac{A\Delta}{\dfrac{f}{\sqrt[3]{M}} - \varepsilon g}, \tag{10}$$

and

$$S \propto \frac{f M^{2/3} - \varepsilon M g}{a_1\, \Delta \rho'\, v^2}. \tag{11}$$

A relation, determined by questions of mechanical strength, exists between L, S, Δ and M. The thickness Δ must be the greater, the greater L and M. The situation is similar to the problem of the thickness of a branch of a tree or the length of the trunk of an animal. Thus

$$F(L\,, S\,, M\,, \Delta) = 0\,. \tag{12}$$

Equations (10), (11) and (12) give us the size of the wing in terms of M and $\overline{v}$, since $\overline{v} \propto v$.

Equation (10) shows that there is a limit of the mass of a bird. For when $M > f^3/\varepsilon^3\, g^3$, L becomes infinite. The actual limit is of course much below $(f/\varepsilon g)^3$, since for structural reasons the length of the wing cannot exceed a certain size, which is of the order of magnitude of the size of the body. With $f \infty 10^5$, which we obtain by considering that the cross section of the muscles in question is about 1% of the cross section of the body, $(f/\varepsilon g)^3 \infty 10^9\ gm = 10^6\ kg$.

If $\Delta \propto L$, then L and S cannot be determined from equations (8) and (9), since only the product LS enters into them. In that case equation (9) gives us LS, while equation (10) establishes a relation between the different parameters, which must hold, in order that flying should be possible at all. In particular, putting $\Delta = \beta L$, we have

$$c_a = \frac{a_1 g \beta \rho'}{\rho\left(\frac{f}{\sqrt[3]{M}} - \varepsilon g\right)}, \tag{13}$$

which shows that the larger M the greater must be c_a. Hence for larger animals, like birds, the profile of the wing must be much more perfect an aerodynamic profile, than for insects. Actually this is the case, the wing of a bird being much more perfect aerodynamically, than the wing of an insect.

Actually in equation (8) we may have more generally a "less than" sign instead of an equality sign. This, with $\Delta = \beta L$ will result in a "greater than" sign in expression (13). Thus the conditions imply inequalities rather than rigid equalities.

To give one illustration of the above: The load per square cm in birds is of the order of $0{\cdot}4 - 1{\cdot}5$ gm cm^{-2} or $4 \times 10^2 - 15 \times 10^2$ dyn cm^{-2}. With velocities of the order of 10^3 cm sec^{-1}, this gives values of c_a between $0{\cdot}6$ and 2. For insects, the load per cm^2 is $\frac{1}{10}$ to $\frac{1}{100}$ of the above. With velocities of the same order of magnitude, this gives a correspondingly smaller c_a.

For approximately similar animals the mass varies as the cube of the linear dimensions l, while the area of the wings varies as l^2. Hence the load per unit area varies as l. The velocity v varies as $l\nu$, hence the resistance as $l^2v^2 = l^4\nu^2$. The acceleration varies as $l\nu^2$, and the mass of the wing as l^3, hence the inertial force varies as $l^4\nu^2$ also. The sum of the resistance and inertial force must be proportional to the muscular force, which being proportional to the cross section of the muscles varies as l^2. Hence

$$\nu^2 l^4 \propto l^2,$$

or remembering that l is proportional to the load m per cm^2 of the wing

$$\nu \propto 1/l; \ \nu \propto 1/m. \tag{14}$$

These relations hold, however, only for similarly built animals. In approximately similarly built insects it is actually observed that the larger the animal the smaller ν, so that at least qualitatively relation (14) is verified. (v. Buddenbrock, 1930, p. 353).

If, however, we consider animals which have approximately the same mass but wings of different sizes we obtain a different relation. The inertial and resistance forces are again proportional to $l^4\nu^2$. But the muscular force is now roughly constant. Hence $\nu^2 l^4 =$ Const and $\nu \propto 1/l^2$. But for constant mass, l^2 is inverse proportional to the load m per cm² of the wing. Hence instead of the second relation in (14), we have:

$$\nu \propto m\,. \qquad (15)$$

Relation (15) is very well verified by observation for some insects (Figure 14), although they appreciably differ from each other with respect to their mass.

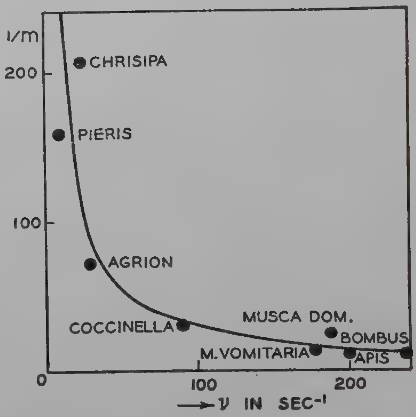


FIGURE 14. Frequency ν of wing beats of some insects plotted against the inverse of load per cm² of wing. Experimental points compared with the theoretical curve. Adapted from Buddenbrock (1930, p. 354).

It is remarked, however, that larger insects fly more rapidly than smaller ones. This at first seems to contradict the above considerations, since $v \propto l\nu =$ const. But we must remember that v differs from $\vec{v}$. The coefficient of proportionality between v and $\overline{v}$, apparently varies with size. This is still a problem to be studied.

If we compare the empirical values of c_a and c_w for aerodynamical profiles and for plane plates, we find (Betz, 1927, pp. 285-287), that a value of $c_a \backsim 1$ may be obtained with either. However in order to obtain such a high value of c_a for a plate, α must be taken rather large. Then c_a turns out to be about ten times as large for a plate as for a profile. For larger animals, like birds, a wing in form of a flat plate would require very high energy expenditure and great force, due to a high c_w. For insects c_a may be about ten times lower. Therefore a flat plate can be used with a much smaller α, in which case c_w will also be reduced correspondingly. Thus insects may have smaller c_a than birds, but approximately the same c_w. The resistance, as we have seen, varies as $l^4\nu^2$, c_w determining the coefficient of proportionality. Muscular force varies as l^2. The relation $\nu = 1/m$ (equation 15) should hold over the whole range of birds and insects, if c_w is about the same.

If $\Delta \propto L$ and only LS is determined, then the determination of L and S separately is made in the following way. For a given LS, the induced resistance will be the smaller the greater L. Hence c_w is itself a function of L and S separately. Thus, we still have two equations for the two variables L and S, although they will be rather unmanageable. In general L should be taken as large as is compatible with structural requirements, such as lead to equation (12).

If the velocity v is to be sustained, then we have an equation which relates that velocity to q. The work done by the force F_r per unit time is for the two wings:

$$2\,\overline{v}\,F_r = c_w\,\rho\,LS\,v^3\,. \tag{16}$$

The work done by F_i per unit time is approximately

$$L^3S\,\nu^2\,\Delta\,\rho'\,. \tag{17}$$

Hence per unit time, because of (3):

$$L^3\,\nu^3\,S\,\Delta\,\rho' = \Delta\,\rho'\,S\,v^3\,. \tag{18}$$

The sum of (17) and (18) must be equal to Mq, if Mq is the excess metabolism over the resting one. Hence

$$(\Delta\,\rho' + c_w\,\rho\,L)\,S\,v^3 = M\,q\,. \tag{19}$$

Since L, S and Δ are determined from (10), (11) and (12), equation (19) gives a relation between q, M and v. Hence q and M alone determine the motion and form of the animal.

Now we shall briefly outline a more detailed but very rough approach to the problem of flight of birds.

In glancing over the graphs, representing the empirical relations between c_a and α (angle of attack) and c_w and α (M. H. Fischer, 1930, p. 323) we find that with some approximation, within a fairly wide range of α's, we have:

$$c_a = A + B\,\alpha; \quad c_w = C + D\,\alpha^2\,. \tag{20}$$

Let (Figure 15) the bird hold the wing at an angle β to the vertical and swing it downwards. The resulting forces will move the wing forward, so that its resulting velocity will be v, making an angle ϕ with the vertical. The vertical force due to the lift F_A and resistance F_w is equal to

$$F = F_A \sin\phi + F_w \cos\phi\,, \tag{21}$$

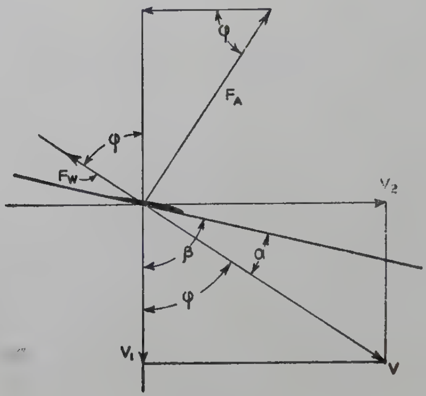


FIGURE 15

and is directed upwards. In order to move the wing down, it is necessary to apply a downward force F_v. If M_w is the mass of the wing, and v_v its instantaneous vertical velocity, then

$$M_w \frac{dv_v}{dt} = F_v - F. \tag{22}$$

Let v_1 (Figure 15) be the *average* vertical velocity, then the duration t_1 of a downward stroke is approximately

$$t_1 = L/v_1. \tag{23}$$

Hence the average acceleration is

$$\bar{\dot{v}}_1 = v_1^2/L. \tag{24}$$

Averaging equation (22), we have

$$\frac{M_w v_1^2}{L} = F_v - F. \tag{25}$$

But

$$F_v = f M^{2/3}. \tag{26}$$

On the other hand for each wing:

$$F_A = \tfrac{1}{2} c_a \rho L S v^2; \; F_v = \tfrac{1}{2} c_w \rho L S v^2. \tag{27}$$

Hence, introducing (20) into (27), the latter into (21), and the latter with (26) into (25), we have

$$\frac{M_w v_1^2}{L} = fM^{2/3} - \rho LS\{[A + B(\beta - \phi)] \sin \phi + [C + D(\beta - \phi)^2] \cos \phi\} v^2. \tag{28}$$

Furthermore we have:

$$v_1 = v \cos \phi \,. \tag{29}$$

The sum of the horizontal components of F_A and F_w is:

$$F' = F_A \cos \phi - F_w \sin \phi \,, \tag{30}$$

and must be positive.

If M is the mass of the bird, and R the coefficient of resistance of the body to the horizontal movement, we have, denoting by v_{h1} the velocity of the body in the horizontal direction

$$M \frac{d v_{h1}}{dt} = F' - R \, v^2_{h1} \,. \tag{31}$$

Since the duration of the down stroke period is given by (23), the average acceleration is

$$\bar{\dot{v}}_{h1} = \frac{\bar{v}_{h1}}{t_1} = \frac{v_1 \, \bar{v}_{h1}}{L} \,. \tag{32}$$

Equation (31) now gives

$$\frac{M v_1 \, \bar{v}_{h1}}{L} = F' - R \, \bar{v}_{h1} \,. \tag{33}$$

We also have the requirement that, approximately at least,

$$F = M g \,. \tag{34}$$

Expressing in (33) and (34) F' and F in terms of v, LS, β and ϕ, we thus have four equations, (28), (29), (33) and (34), which determine v, LS, ϕ and $\bar{v}_{h1} (< v_1)$ for a given β. The distance traveled during the down stroke period is

$$\bar{v}_{h1} \, t_1 = \frac{L \, \bar{v}_{h1}}{v_1} \,. \tag{35}$$

For the upstroke we can consider the movement of the wings relative to the body as slow, and compute the loss of velocity and gain of altitude by putting

$$M \frac{d v_{h2}}{dt} = - \left(c_w \, \rho \, LS + R \right) v^2_{h2} \,. \tag{36}$$

Easily integrated, (36) gives v_{h2} as a function of time, with the initial conditions $v_{h2}(0) = \bar{v}_{h1}$. c_w is now to be taken for a different α. The duration of the upstroke period is given by the requirement, that

$$c_a \rho LS v^2_{h2} \geqq Mg . \tag{37}$$

The moment when the inequality (37) ceases to hold, the new down stroke must begin.

The duration t_1 and t_2 of the two periods thus known, as well as the average velocities during those periods, the total average velocity $\overline{v}$ is obtained in terms of M, L, S, α_1, α_2 etc.

The angle α may be chosen so as to maximize $\overline{v}$.

VIII. The Internal Structure of Animals

The size and shape of different internal organs may also be considered as determined by the requirements put on them by the performance of their functions. Hence a general physicomathematical theory of organic form should include the internal structure of animals as well as their external shape. A step in that direction is to be made in this section, which, however, must be left even sketchier than the preceding ones.

If the mass M and the maximum sustained velocity of an animal are given and if we denote by q^* the metabolic rate necessary to supply the energy for sustained locomotion, then, for the case of a quadruped or biped, the value of q^* is given by equation (49) of section *IV*. But a continuous supply of the energy $Q = Mq^*$ per unit time requires a definite continuous supply of oxygen. If V_L denotes the amplitude of the volume of the lungs, and ν_L the frequency of respiration, then the supply of oxygen is proportional to $\nu_L V_L$. But the oxygen supplied goes not only for the energy supply of the running mechanism, but also to supply the energy Q_L necessary to maintain the movements of the lungs, the energy Q_c, necessary to maintain the circulation of the blood, the energy Q_i, necessary to maintain the peristaltic movements of the intestinal tract, and the energy $Q_0 = Mq_0$, necessary to maintain the nonmobile cells of the organism. Denoting therefore by a_1 and a_2, two coefficients, which are determined by the efficiency of the lung (a_1), and by the energy equivalent of the oxygen, we have

$$a_1 \nu_L V_L = a_2 (Mq^* + Q_L + Q_c + Q_i + Q_0). \tag{1}$$

But the maximum frequency ν_L is determined by V_L. The latter determines the size of the musculature that contracts and expands the lungs. This size determines first of all the possible force acting on the lungs, as well as the viscous resistance of the muscles. By appropriate mechanical considerations, involving possibly also the inertial terms, we shall arrive at an equation

$$\nu_L = f_L(V_L). \tag{2}$$

Furthermore, if ν_L and V_L are given, the rate Q_L of energy supply necessary to maintain the periodic contractions and expansions of the lungs is also given:

$$Q_L = F_2(\nu_L, V_L). \tag{3}$$

The adequate supply of oxygen is provided also by the circulatory system. Denoting by V_c the effective volume of the heart per beat, and by ν_c the frequency of heart-beats, we see that $\nu_c V_c$ is proportional to the sum of all the Q's. Hence with a_3 as a constant

$$\nu_c V_c = a_3(Mq^* + Q_L + Q_c + Q_i + Q_0). \tag{4}$$

And again we have

$$\nu_c = f_c(V_c), \tag{5}$$

where f_c is different from f_L.

For Q_c we must remember that it depends not only on ν_c and V_c, but also on the size and structure of the blood vessels. For the same ν_c V_c, Q_c will be greater, the longer the total lengths l_c of the circulatory circuit and the less its effective cross section s_c. Thus

$$Q_c = F_c(\nu_c, V_c, l_c, s_c). \tag{6}$$

But l_c is determined by the overall length of the body L, and of the extremities l. Thus

$$l_c = f_1(L, l). \tag{7}$$

Similarly, the value of s_c is determined by the total size of the animal. For an adequate supply of all tissues with oxygen and adequate removal of waste products, there must be so many capillaries per unit volume, and they must be of a given size, to have the necessary surface. Hence

$$s_c = f_2(M). \tag{8}$$

Denoting by l_i and s_i the length and average radius of the intestinal tract, we find that the total area $2\pi l_i s_i$ must be proportional to $(Q_0 + Q'_L + Q'_c + Q'_i)$, where Q'_L, Q'_c, Q'_i denote the necessary energy supply to the lungs, heart and intestines in a resting organism, that is when $q^* = 0$. The reason for the proportionality is the necessity of a given rate of resorption, which we assume to be proportional to the surface. Hence

$$2\pi l_i s_i = a_4(Q_0 + Q'_L + Q'_c + Q'_i). \tag{9}$$

Similarly, the volume of the intestinal tract is determined by the same quantity, since the latter determines the amount of food that must daily be held in the intestinal tract:

$$l_i s_i^2 = f_i(Q_0 + Q'_L + Q'_c + Q'_i). \tag{10}$$

Also we have

$$Q'_i = F_i(l_i, s_i). \tag{11}$$

The length of the body may be determined by mechanical considerations from its mass M, as has been done in section *III*. We have in general

$$L = F_2(M). \tag{12}$$

For the thickness s_e of the legs we have, as in section *III*:

$$s_e^2 = a_5 M, \tag{13}$$

and finally we have expression (62) of section *IV*, giving l in terms of the maximum velocity $\bar{v}$:

$$l = a_6 \bar{v}^2. \tag{14}$$

For an animal at rest, $q^* = 0$, and $Q_L = Q'_L$, $Q_c = Q'_c$, $Q_i = Q'_i$. The latter remains also for $q^* > 0$, when the animal runs.

Putting $q^* = 0$ into equation (1) and (4) we have 14 equations for the determination of the 14 quantities:

$$\nu'_L, V'_L, Q'_L, Q'_c, Q_i, \nu'_c, V'_c, l_c, s_c, l_i, s_i, L, s_e, l \tag{15}$$

in terms of M, q^* and $\vec{v}$.

Returning now to the original equations with $q^* > 0$ and when it is given by equation (49) of section *IV*, equations (1), (2), (3), (4), (5) and (6) give us 6 equations for the determination of the 6 quantities:

$$\nu_L, V_L, Q_L, Q_c, \nu_c, V_c. \tag{16}$$

Thus, M and q_0 determine not only the general shape of the animal, but also its internal structure.

Strictly speaking, relations (2) and (5) will involve m_L and m_c, the masses of the lungs and of the heart correspondingly. These may be left as undetermined parameters. Then, according to the principle of maximum simplicity, we shall take for m_L and m_c the smallest values, which permit real positive solutions (15) and (16) of our equations. That such minimum values of m_L and m_c, different from zero, must exist, is physically obvious.

Establishment of the form of f_L (equation 2), F_L (equation 3), f_c (equation 5), F_e (equation 6), etc. form the main part of our problem. This is to be done through a theory of lung and heart activity.

We may introduce equations for other organs. Thus the mass m_k of the kidney will be determined by the maximum metabolism $\sum_k Q_k$ which determines the necessary excretion. The mass of the liver will be at least partially determined by the amount of glycogen stored, which may be mobilized during running, to supply the necessary q^*.

Notice that $\sum_k Q'_k$ represents fundamentally the basal metabolism. It may be possible that expressed as a function of M, $\sum_k Q'_k$ will vary approximately as $M^{2/3}$, in spite of the fact that $Q_0 \propto M$. If this were so, we would have Rubner's law derived from the above equations.

In the above considerations we have entirely disregarded the skeleton as an internal structure. We may introduce it in the following manner.

Instead of (12) we shall have, denoting by L_s and s_s the length and thickness of the spine,

$$L_s = F_2(M, s_s)\,; \tag{17}$$

this may be subject to the condition that the ratio

$$R = \frac{L_s\, s_s^2}{M} \tag{18}$$

would have a minimum. Expressing L_s in terms of M and s_s from (17), we find:

$$R = R(M, s_s)$$

and determine s_s from

$$\frac{\partial R}{\partial s_s} = 0. \tag{19}$$

This would be in line with the principle of maximum simplicity, for it will give us the minimum weight ($\propto$ volume) of the skeleton.

Relation (13) should, strictly speaking, determine the cross section of the bones of the extremity. The muscular cross-section may be argued to be proportional to the latter, because the stronger the bones of the legs, the stronger muscular forces and torques they may support without breaking.

Equations (49) and (62) of section IV both contain the angle ϕ. The requirement that both maximum and sustained values of $\overline{v}$ should be the same eliminates ϕ, giving a relation between q, $\overline{v}$ and l, which takes place of equation (14).

If we add

$$M = \sum M_L + M_c + M_i + M_s$$

we may perhaps eliminate one of the three determining parameters.

As a matter of illustration only, without any claim to any correspondence to real situation, we shall briefly outline a possible theory of the lungs and heart.

Let us consider the plausible case, that Q_L, Q_c and Q_i are negligible compared to $Mq^* + Q_0$, and let the latter roughly follow Rubner's law, being proportional to the surface of the animal, or, for similar animals, to $M^{2/3}$. Then

$$V_L \nu_L \propto M^{2/3} . \tag{20}$$

Let us also assume, that the volume V_L is proportional to the mass M_L of the lungs. The linear dimensions are then proportional to $M_L^{2/3}$, and the acceleration in the periodic breathing movements are proportional to $M_L^{1/3} \nu_L^2$. Hence the inertial forces are proportional to $M_L^{4/3} \nu_L^2$. Since the muscular forces of the lungs vary approximately like the cross section of the muscles, they will be roughly proportional for similarly built lungs to $M_L^{2/3}$. As the lung pumps air back and forth, it has to overcome the resistance of the air flow through all the parts of the lung. That force of resistance may be taken as roughly proportional to the total pressure, which is proportional to the volume velocity $V_L \nu_L \propto M_L \nu_L$. The force of resistance will also be proportional to the total area S in which that pressure is exerted. If the size and number of alveoles per cm^3 is roughly constant, then $S \propto V_L \propto M_L$, and the resistance force is proportional to $M_L^2 \nu_L$. Since the muscular force must be equal to the sum of the inertial forces and of the forces of air resistance, we have, denoting by a and b two coefficients:

$$M_L^{4/3} \nu_L^2 + aM_L^2 \nu_L - bM_L^{2/3} = 0 . \tag{21}$$

From (20) and (21) we have, remembering that $V_L \propto M_L$:

$$M^{4/9} \nu_L^{5/3} + aM^{8/9} - b\nu_L^{1/3} = 0 . \tag{22}$$

The graph of equation (22) is represented on Figure 16. From it we see that it has two positive roots, one increasing with M, the other decreasing. It follows from (20) that the smaller root, which increases with M, gives a larger value of M_L. By the principle of maximum simplicity of structure, we must therefore choose the larger root, which gives a smaller size of lung.

A very rough solution of equation (22) may be obtained in the following way.

Put

$$\nu_L{}^{1/3} = x\,;\ M^{4/9} = A\,. \tag{23}$$

Equation (22) now becomes

$$Ax^5 - bx = -a_1A^2\,. \tag{24}$$

The abscissa of the minimum of the left side is

$$x_m = \alpha\left(\frac{b}{A}\right)^{1/4} \tag{25}$$

where α is a numerical coefficient. The ordinate of that minimum is

$$y_m = (\alpha^5 - \alpha)\,b\left(\frac{b}{A}\right)^{1/4}. \tag{26}$$

The point x_0 of intersection of the left side with the axis of abscissa is:

$$x_0 = \left(\frac{b}{A}\right)^{1/4}. \tag{27}$$

Very roughly we may approximate the portion y_mx_0 of the curve (Figure 16) by a straight line passing through those points. The equation of this straight line is

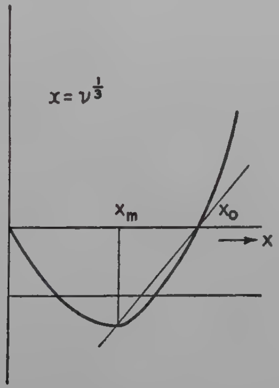


FIGURE 16

$$Bx - B\left(\frac{b}{A}\right)^{1/4} = y\,;\ B = \frac{b\,(\alpha^5 - \alpha)}{1 - \alpha}.$$

Substituting that for the left side of (24) we find

$$x = -\frac{a_1}{B}A^2 + \left(\frac{b}{A}\right)^{1/4}. \tag{28}$$

For not too large masses, the second term of the right side of (28) prevails, and, remembering (13) we find:

$$\nu_L \propto M^{-1/3}\,. \tag{29}$$

From (29) and (20) we find

$$M_L \propto M\,. \tag{30}$$

Relations (29) and (30) are fairly well satisfied by actual data, as seen from Figures 17 and 18.

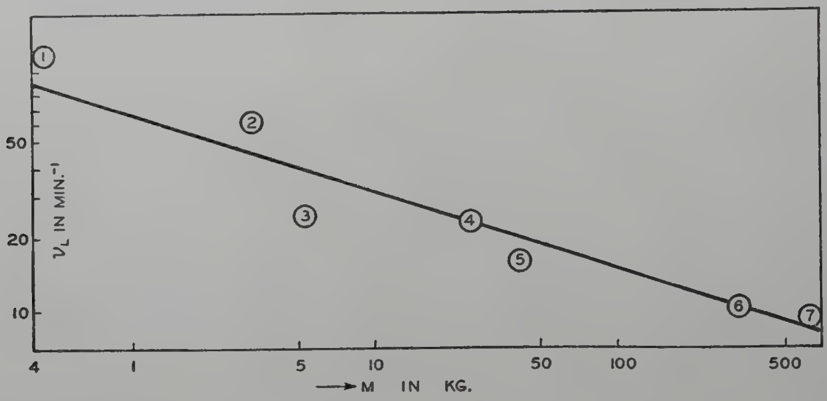


FIGURE 17. Frequency ν_L of breathing plotted against mass M of the animal on logarithmic scale. The straight line has the theoretically required slope of — 1/3. 1 — rat; 2 — rabbit; 3 — cat; 4 — dog; 5 — sheep; 6 — bear; 7 — horse. Data from Crile (1941) and Oppenheimer and Pincussen (1926, p. 476).

An interesting problem is presented in this connection by the lungs of birds. Their relative size is rather small, compared to those of mammals. But their structure and their mechanism of action are apparently more complicated (A. Bethe, 1925). The lung seems to be bathed by a continuous stream of air, due to a peculiar mechanism. From considerations of diffusion it can be readily seen that the ventilating efficiency of a bird's lung is several times higher than that of a mammal. This permits a smaller volume, which is essential in a bird in order to reduce weight and give room for the muscles operating the wings. It may perhaps be possible in the future to show mathematically, by developing a more exact theory of the lungs, that a lung of the mammal's type would be incompatible with flying and other functions of the birds, and that the structure of the bird's lung is the simplest that satifies the necessary requirements.

Somewhat similar considerations may be made about the heart.

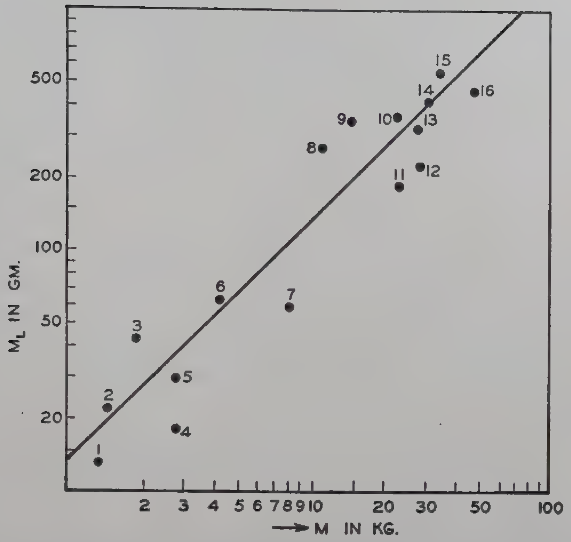


FIGURE 18. Mass M_L of lungs plotted against mass M of animal on logarithmic scale. The straight line has the theoretically required slope of 1. 1 — cat; 2 — cat; 3 — hare arctic; 4 — hare african; 5 — jackal; 6 — beaver; 7 — coyote; 8 — dog; 9 — dog; 10 — greyhound; 11 — police collie; 12 — capibra; 13 — mountain lion; 14 — huskies; 15 — jaguar; 16 — leopard. Data from Crile (1941).

Consider a capillary of length l and radius r. Let that capillary supply with oxygen a region of radius R and length l. Denoting by $\bar{c}$ the average oxygen concentration in the capillary, assuming no radial gradients, and denoting by c^* the concentration of oxygen in the tissue, by h the permeability and by αq the rate of oxygen consumption per cm^3 per sec. proportional to the rate of energy metabolism q, we have

$$2\pi r l h(\bar{c} - c^*) = \pi(R^2 - r^2) l \alpha q \,, \tag{31}$$

or

$$R^2 = r^2 + \frac{2rh}{\alpha\, q}(\bar{c} - c^*) \,. \tag{32}$$

If $\bar{c}$ and c^* are considered as approximately constant, then for a given r equation (32) gives R. The higher q, the smaller R, hence the larger the number of capillaries per cross section of tissue. Since q increases with decreasing mass, according to Rubner's law, smaller animals should have a larger number of capillaries per unit cross section of tissue. This seems to be the case (Oppenheimer and Pincussen, 1925, p. 121).

If v denotes the velocity of blood flow, then $\pi r^2 v \bar{c}$ is the amount of oxygen entering the capillary at the arterial end. Considering for simplicity that at the venous end the concentration of oxygen is zero (the general case is treated similarly) we have:

$$\pi r^2 v\bar{c} = 2\pi r l h(\bar{c} - c^*), \tag{33}$$

or, putting

$$\bar{c} - c^* = c . \tag{34}$$

$$vr\bar{c} = 2lhc , \tag{35}$$

or

$$v = \frac{2lhc}{r\bar{c}}. \tag{36}$$

From Poiseuille's law we have for the pressure difference along the whole capillary:

$$\Delta p = a\frac{lv}{r^2};\ a = 8\mu;\ \mu - \text{viscosity}. \tag{37}$$

Equations (36) and (37) give

$$\Delta p = b\frac{l^2}{r^3}, \tag{38}$$

where

$$b = \frac{2hac}{\bar{c}}. \tag{39}$$

Most of the blood pressure is across the capillaries. If we schematize the circulatory circuit, as shown on Figure 19; we see that (38) gives approximately the average blood pressure. Approximately, in similarly built animals, the length l of the capillaries varies like the linear dimensions of the animal or like $M^{1/3}$. If r is the same for all animals, then $\Delta p \propto M^{2/3}$. Actually Δp varies little with M , within a rather wide range of M's. (Oppenheimer and Pincussen, 1925, p. 143). Hence, if Δp is approximately constant, we must have:

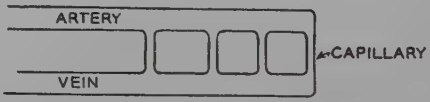


FIGURE 19

$$r^3 \propto l^2 . \tag{40}$$

There may be different reasons for such a relation. They may be purely mechanical. A larger capillary may have to be thicker in order not to break due to natural stresses, to which it is subjected by the tissues.

One might think that an upper limit for r is set by the requirement that the radial gradients should be very small. If c_1 and c^2 are the concentrations on the axis and at the periphery of the capillary, so that

$$\bar{c} = \frac{c_1 + c_2}{2}, \tag{41}$$

then we have, denoting by D the diffusion coefficient,

$$\pi r l \frac{2D(c_1 - c_2)}{r} = 2\pi r l h (c_2 - c^*), \tag{42}$$

or

$$\frac{c_1 - c_2}{c_1 - c^*} = \frac{r\,h}{D}. \tag{43}$$

If

$$\frac{c_1 - c_2}{c_2 - c^*}$$

should be below a small quantity ε, we have

$$r \leqq \frac{D\,\varepsilon}{h}.$$

This does not connect r with l in any way.

To derive equations for the size and frequency of the heart, we may argue as follows:

Assuming the beat volume of the heart to be roughly proportional to the actual maximum volume V_c, and denoting by ν_c the frequency, we have:

$$V_c \nu_c \propto Mq \propto M^{2/3}, \tag{44}$$

according to Rubner's law.

The mass of the heart is proportional to V_c, its linear dimensions to $V_c^{1/3}$. Hence the acceleration is proportional to $V_c^{1/3}\,\nu_c^2$, and the inertial force to $V_c^{4/3}\,\nu^2$. The total force necessary to overcome the blood pressure p is proportional to $pV_c^{2/3}$. The mechanical force of the heart muscle is proportional to $V_c^{2/3}$, their cross section. Hence denoting by a, b and c coefficients of proportionality, we have

$$aV_c^{4/3}\,\nu_c^2 + bpV_c^{2/3} = cV_c^{2/3}, \tag{45}$$

or

$$V_c^{2/3}\,\nu_c^2 = A;\ A = \frac{c - bp}{a}. \tag{46}$$

Equation (44) solved for V_c, and introduced into (46) gives:

$$\nu_c = \frac{A^{3/4}}{M^{1/3}}, \tag{47}$$

and

$$M_c = \frac{M}{A^{3/4}}. \tag{48}$$

To what extent relations (47) and (48) are actually satisfied in nature is shown on Figures 20 and 21.

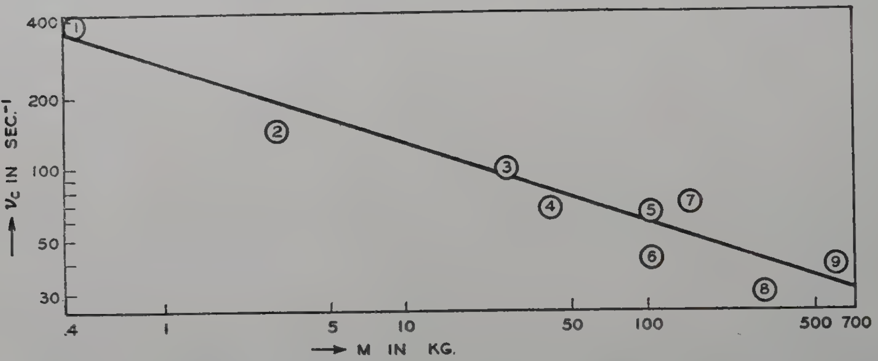


FIGURE 20. Heart frequency ν_c plotted against mass M of the animal on logarithmic scale. The straight line has the theoretically required slope — 1/3. 1 — rat; 2 — rabbit; 3 — dog; 4 — sheep; 5 — tiger; 6 — lion; 7 — pig; 8 — camel; 9 — horse. Data from Crile (1941) and Oppenheimer and Pincussen (1925), p. 138).

IX. Some Remarks on Unicellular Organisms

If the principle of determination of structure by function is to hold generally, it should apply also to single cells. Physicochemical functions are more likely to be of importance here, than locomotion. The determining variables may be different chemical parameters. The rates of reactions are dependent on the concentrations of metabolites, and the average concentrations of those are determined by the solutions of the diffusion equations, which involve the geometrical shape and structure of the system. The solution of the fundamental problem of the nucleus and cytoplasm may be sought in that direction. If a cell of given mass is to be the seat of certain reactions, which are quantitatively specified as to their rates, and if that cell is

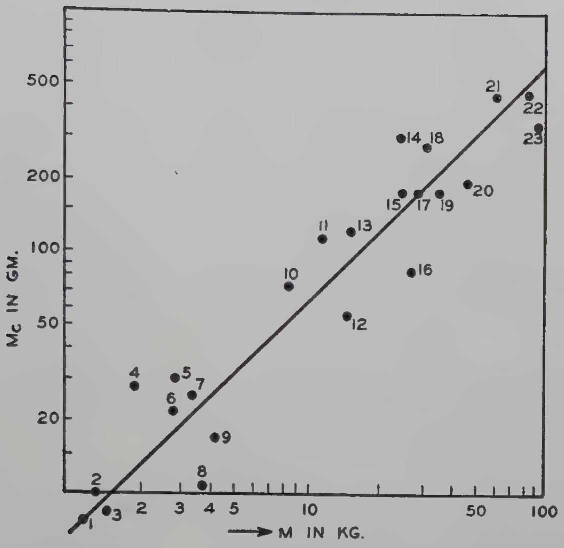


FIGURE 21. Mass M_c of heart plotted against the mass M of the animal on logarithmic scale. The straight line has the theoretically required slope 1. 1 — cat; 2 — agouti; 3 — cat; 4 — hare arctic; 5 — hare african; 6 — jackal; 7 — fox; 8 — rabbit; 9 — beaver; 10 — coyote; 11 — dog; 12 — capibra; 13 — dog; 14 — greyhound; 15 — police collie; 16 — capibra; 17 — mountain lion; 18 — huskies; 19 — jaguar; 20 — leopard; 21 — hyena; 22 — lion; 23 — lion. Data from Crile (1941).

characterized by the presence of catalists, which control those reactions, then it may well happen that the necessary results may be obtained *only* if some catalists and some reactions are spatially segregated in a region which we call nucleus. A number of new problems in cellular biophysics are suggested by such considerations.

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